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THE URINARY EXCRETION OF PENICILLIN AFTER INGESTION WITH AND WITHOUT ADJUVANTS AND FOLLOWING INTRAMUSCULAR INJECTION[1]

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In their classic paper Florey and co-workers (1) found that a large part of the antibacterial effectiveness of penicillin was lost when the drug was taken orally as compared with parenteral administration. This has since been confirmed by numerous investigators (2, 3, 4, 5, 6, 9, 11, 12, 13). It has generally been thought that successful administration of penicillin by mouth could be accomplished by protecting it from destruction by gastric acidity. Several studies have been reported in which attempts were made to circumvent this assumed mechanism of destruction either by neutralizing the gastric acidity by various antacid adjuvants taken with the penicillin or by encapsulating it in such a manner that it would not be released until it had reached the less acid or even slightly alkaline medium of the intestine.

Sodium bicarbonate ingested with or prior to penicillin (1, 5, 15) failed to protect most of the drug from destruction. Little and Lumb (8) reported that when penicillin mixed with raw egg white was ingested 10 minutes after taking sodium bicarbonate with milk the urinary excretion of the drug was comparable to that after a like dose injected intramuscularly; but Heatley (9) was unable to confirm their results, although he did find that the urinary excretion after taking the dose in egg white was more than double that when taken in water alone. Charney et al (5) gave penicillin orally with trisodium citrate, disodium phosphate, Amphojel (hydrous alumina), and milk with calcium carbonate, but only the trisodium citrate and the disodium phosphate in the fasting state increased the amount recoverable in the urine to only about one-third that which would have been excreted had the same dose been given intramuscularly (2, 22). The hydrous alumina gave an intermediate value when compared with the controls. In the absence of trisodium citrate only five per cent of the dose of penicillin taken after breakfast appeared in the urine whereas eleven per cent was excreted when the dose was taken with suitable amounts of trisodium citrate after breakfast. Even so this was only about one-fifth the amount which would have appeared in the urine had the dose been injected intramuscularly. Welch and co-workers (23) reported therapeutic blood levels of penicillin which were maintained for prolonged intervals of time after the ingestion of penicillin solutions to which suspensions of aluminum hydroxide or magnesium hydroxide were added dropwise. When 100,000 units thus treated with aluminum hydroxide were taken by eleven subjects the average recoverable in the urine during the next twenty-four hours was only

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13.6 per cent of the dose. These findings are supported by the findings of Charney et al (5) as well as by the present report. McDermott and co-workers (6) gave sufficiently large amounts of magnesium trisilicate over a period of three hours to change the pH of the stomach contents to about 8.0 before giving penicillin in water, in peanut oil, and in corn oil plus beeswax. The average urinary excretion during the next two hours was about twelve per cent in each case although there were indications that the oils delayed the excretion somewhat. György and his associates (7) reported mixed results in the clinical use of oral penicillin with trisodium citrate. With doses of penicillin comparable to those customarily given parenterally the combination was effective in the treatment of gonoccic urethritis in males as well as in a few other clinical conditions, but doses as high as 300,000 units (0.18 gm.[3]) given orally in combination with trisodium citrate brought about only temporary clinical improvement of gonoccic vaginitis in young girls even after three such courses of treatment whereas permanent cures were obtained when the same dose was administered intramuscularly. Krantz and co-workers (14) reported effective serum levels of penicillin after oral administration with basic aluminum aminoacetate. However, the effectiveness of this antacid is impossible to evaluate on the basis of their paper since the results of the control experiments where penicillin was taken by the same subjects without the antacid were not disclosed.

Florey et al (1) first suggested that the destruction of penicillin by gastric acidity might be prevented by using enteric-coated capsules but their attempts to use phenyl salicylate coated vehicles were unsuccessful. Burke (12) and his associates sealed penicillin in a capsule which was then surrounded by a second capsule that was treated by immersion in diluted formaldehyde for five seconds followed by 95 per cent alcohol for five minutes. The ingestion of 100,000 units (60 mg.[3]) in these capsules gave serum levels of penicillin comparable to those reported by others after the parenteral administration of 40,000 units. Libby (19) suggested the administration of penicillin by mouth suspended in digestible oils contained in enteric-coated capsules. In experiments in which the results of suitable controls were not reported, he found that therapeutic blood levels of penicillin were attainable by giving gelatin capsules containing 90,000 units of the calcium or sodium salt of the drug suspended in cottonseed oil. In view of the results reported by McDermott et al (6) it is probable that Libby would have found no therapeutic advantage to the use of the suspensions in oil had he tried either penicillin in capsules without the oil or simple aqueous solutions. (See under discussion of Table I). Recently Perlstein et al (21) gave penicillin calcium suspended in equal parts of lanolin and corn oil in gelatin capsules by mouth and found that the urinary excretion was thereby prolonged. However, the average total recovery was only about fifteen per cent or about one-fourth of what it would have been had the same amount been injected intramuscularly (2, 22).

In the following studies penicillin was taken by mouth in conjunction with various antacids and other adjuvants in attempts to decrease the destruction within the stomach and intestine so that the amounts recoverable in the urine might be made to approach or equal those recoverable after intramuscular administration. The results with a single subject are reported to avoid the confusion the data would present had the findings with several subjects been considered. It will be shown below that a remarkable constancy in the rate of excretion as well as the total amount of penicillin excreted occurred at different times in the same subject

[3]Since the international unit of penicillin has been defined as 0.6 microgram of the International Standard consisting of the pure crystalline sodium salt of penicillin G or II (17, 18), it has been proposed (16) that penicillin dosages might be expressed advantageously on the basis of the weight of the pure principle present in preparations now on the market rather than by the cumbersome unitage method. The situation is analogous to that proposed by Waksman (10) for expressing quantities of streptomycin used clinically.

under comparable experimental conditions. To avoid frequent, repeated venipunctures as well as the assay difficulties encountered in determining concentrations of penicillin in the blood, assays were carried out in triplicate by the Oxford Cup Method[4] on voided urines collected at standardized intervals throughout all of the experiments. This procedure permitted screening tests to be carried out very readily. The assumption on which it is based is supported by the work of Rantz and Kirby (15) who found that several-fold differences in the rate of urinary flow in certain subjects were not associated with variations in the plasma clearance of penicillin injected intravenously and that the rate of excretion was proportional to the plasma concentration.

Urinary Excretion after Ingestion of 100,000 Units with and without Adjuvants Compared with Intramuscular Injection

In Expt. 1, the contents of one vial of the sodium salt of penicillin (100,000 units) was dissolved in 20 ml. of sterile normal saline for injection deep intramuscularly at two sites on the thigh. The urine was collected one, two, three, four, six and eight hours later (Table I) and immediately diluted with cold one per cent phosphate buffer, pH 6.0, for assay. The total percentage of the dose recovered, 65.1, as well as the rate of excretion was comparable to the data in the literature (2, 22) after intramuscular administration in other subjects.

Expt. 2 was similarly carried out except that the penicillin was dissolved in only 10 ml. of sterile normal saline and the dose was injected into a single site. The very marked catharsis due to the simultaneous ingestion of five grams of U.S.P. magnesium oxide did not change the total amount excreted in the urine, 59.2 per cent, nor did it alter the rate curve significantly. This may be taken as evidence that the difference between an intramuscular dose and the amount recoverable in the urine is not due to elimination via the feces.

The average of the total amount excreted in the urine in the first two experiments is 62.1 per cent of the intramuscular dose. This value will serve through much of the discussion as a reference with which values obtained after oral administration may be compared.

Expt. 3. When 100,000 units (60 mg.[3]) were taken on an overnight fasting stomach, 11.4 per cent of the dose was excreted in the urine in the first six hours. The results of this experiment wherein a very crude calcium salt of penicillin extracted from a surface culture of a strain of *Penicillium notatum*[5] was ingested should be compared with the 11.2 per cent recovered in Expt. 6 where the same unitage as a highly refined sodium salt of penicillin extracted from a submerged culture of the mold was taken orally. Obviously there was no difference.

The average of the total amount recovered in the urine in Expts. 3 and 6 was 11.3 per cent. Comparison of this value with the average of 62.1 per cent after intramuscular injection reveals that only 18.2 per cent as much appears in the urine after ingestion on a *fasting stomach* as after intramuscular injection in the subject used. In other words five times as much would be required for oral administration *in the fasting state.*

The situation when penicillin was administered orally on a non-fasting stomach in the same subject is illustrated by the data for Expt. 12 where the total excretion was 4.7 per cent of the dose. This means that, based on these data, the subject used would have to ingest thirteen times the intramuscular dose on a *non-fasting stomach* (compare with Expt. 108).

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[4]I am indebted to Marguerite M. Sullivan for these assays.

[5]Obtained from the Northern Regional Research Laboratory.

TABLE I

URINARY EXCRETION OF PENICILLIN AFTER ADMINISTRATION OF 100,000 UNITS

Expt. No.	Route	Date	Conditions under which Penicillin was Administered	Per Cent of Dose Excreted in the Intervals (Hrs.)						Total % of Dose Recovered
				0–1	1–2	2–3	3–4	4–6[4]	6–8	
1	I–M[1]	3/22/45	In normal saline, non-fasting	39.7	15.6	5.1	2.8	1.6	0.3	65.1
2	I–M[1]	3/23/45	In normal saline, non-fasting; 5.0 gram MgO taken at same time in 200 ml. tap water. Marked catharsis when each specimen was collected	28.1	17.8	8.0	2.3	2.4	0.6	59.2
3	Oral[2]	12/6/44	In 200 ml. water on an overnight fasting stomach	4.7	3.5	1.6	1.0	0.6	.....	11.4
4	Oral[2]	12/8/44	Suspended in 75 ml. U.S.P. Cottonseed oil followed by 200 ml. tap water on an overnight fasting stomach	4.5	4.2	1.7	0.7	0.5	.....	11.6
5	Oral[2]	12/12/44	1 mg. Atropine followed 10 minutes later by the penicillin dissolved in 200 ml. cold tap water on an overnight fasting stomach	3.5	3.1	2.5	2.1	1.7[3]	0.4	13.3
6	Oral[1]	3/27/45	In 350 ml. tap water on an overnight fasting stomach	4.7	3.2	1.3	1.1	0.9	.....	11.2
7	Oral[1]	4/4/45	In water on an overnight fasting stomach, 10 minutes after taking 5 gms. $Al(OH)_3$ suspended in water	5.3	4.0	1.5	0.8	0.6	.....	12.2
8	Oral[1]	4/6/45	In water on an overnight fasting stomach followed immediately by 500 ml. tap water at 4° C. Another 200 ml. at 4° C. was drunk when first urine specimen was collected	3.9	3.8	1.2	1.3	1.1	0.2	11.5
9	Oral[1]	4/17/45	Dissolved in whites of 2 eggs 10 minutes following 10 gms. of $NaHCO_3$ dissolved in ½ pint of homogenized milk on an overnight fasting stomach	1.0	5.2	2.3	1.0	2.1	.....	11.6
10	Oral[1]	5/14/45	In water on an overnight fasting stomach 10 minutes after taking 20 gms. of powdered egg white dissolved and suspended in about 400 ml. of tap water	3.5	2.6	2.1	1.5	1.1	0.1	10.9
11	Oral[1]	5/9/45	Dissolved in egg-nog containing 3 egg whites, milk, sugar and vanilla immediately after a breakfast consisting of bacon, egg, toast with butter and hot chocolate made with milk	1.5	3.1	1.3	0.9	1.2	0.2	8.2
12	Oral[1]	5/7/45	In water 40 minutes after breakfast consisting of orange juice, toast and butter, poached egg, and dry cereal with milk and sugar	1.2	1.6	0.9	0.6	0.4	.....	4.7
13	Oral[1]	4/10/45	In water on an overnight fasting stomach 10 minutes following 25 gms. of Wilson Granular Concentrated Mucin washed down with 250 ml. of tap water	2.4	1.7	0.7	0.3	0.2	.....	5.3
14	Oral[1]	5/11/45	Dissolved in 400 ml. water containing 20 gms. glycine on an overnight fasting stomach	2.4	3.7	2.0	0.9	0.6	0.1	9.7
15	Oral[1]	5/16/45	In water immediately following 5 gms. activated charcoal, Merck, suspended in 300 ml. water on an overnight fasting stomach	0.2	0.2	0.2	0.1	0.1	.....	0.8
16	Oral[1]	3/28/45	In 400 ml. water containing 3 gms. trisodium citrate on an overnight fasting stomach	7.0	7.2	2.4	1.4	0.8	.....	18.8
17	Oral[1]	6/13/45	In water on overnight fasting stomach followed immediately by a solution of 5.0 gms. ferric ammonium citrate in about 300 ml. tap water	0.7	3.0	2.4	1.1	0.8	0.2	8.2

TABLE I—(*Continued*)

Expt. No.	Route	Date	Conditions under which Penicillin was Administered	Per Cent of Dose Excreted in the Intervals (Hrs.)						Total % of Dose Recovered
				0–1	1–2	2–3	4–5	4–6[4]	6–8	
18	Oral[1]	6/14/45	In water on overnight fasting stomach followed immediately by a solution of 5.0 gms. d-glutamic acid adjusted to pH=8.0 with NH_4OH in about 300 ml. tap water	2.6	5.2	2.1	0.9	1.0	0.1	11.9
19	Oral[1]	6/15/45	In water on overnight fasting stomach together with an elixir of ammonium citrate[6] calculated to contain 5.0 gms. of the salt in about 250 ml. tap water	3.4	3.1	2.1	1.2	1.0	0.1	10.9
20	Oral[1]	6/19/45	In water on overnight fasting stomach followed immediately by 5.0 gms. of diammonium acid citrate in solution in about 300 ml. tap water	2.0	2.3	0.8	0.4	0.5	0.6	6.6
21	Oral[1]	6/21/45	In water on overnight fasting stomach followed immediately by a suspension of 20.0 gms. of casein in about 500 ml. of tap water	3.6	1.5	1.4	0.8	0.8	0.2	8.3
22	Oral[1]	6/23/45	In water on overnight fasting stomach followed immediately by a suspension of 20.0 gms. of zein in about 400 ml. tap water	2.9	3.3	1.7	1.0	0.9	0.2	10.2
23	Oral[1]	6/27/45	One vial dissolved in 20 ml. water, 30 ml. hydrous alumina (Creamalin, Liquid) slowly stirred in. Immediately drunk on overnight fasting stomach	5.3	5.4	2.3	0.9	0.6	.....	14.5

[1]Penicillin Sodium, deep culture.
[2]Calcium salt containing 54.5 units/mg. surface culture.
[3]Estimated value.
[4]Regular lunch eaten in this interval.
[5]Kindly supplied by the Wm. S. Merrell Co.
[6]13.3 ml. of a solution of 12 gm./fl. oz. of ammonium citrate kindly supplied by the Wm. S. Merrell Co.

Expt. 4. It was felt that suspending the penicillin in a digestible oil might protect it from the destruction by the gastric juice while permitting its release for absorption in the duodenum and jejunum. The results of this experiment, 11.6 per cent, indicate that there was no therapeutic advantage to be gained from suspending penicillin in cottonseed oil for ingestion over giving it in simple aqueous solution. This is in contrast to the inferences of Libby's paper (19) in which the results of suitable control experiments were not reported.

Expt. 5. These data reveal only a slight advantage to the use of atropine with a view to decreasing the destruction by gastric juice of penicillin taken orally.

Expt. 6. Discussed under Expt. 3 above.

Expt. 7. U. S. P. aluminum hydroxide, dried, ingested with the penicillin increased the amount recoverable in the urine slightly to 12.2 per cent. In Expt. 23, 30 ml. of a suspension of approximately 5.5 per cent aluminum hydroxide (Creamalin, Liquid) was slowly stirred dropwise into 100,000 units of penicillin dissolved in 20 ml. of distilled water and immediately drunk on an overnight fasting stomach. This method of mixing increased the amount recoverable in the urine during the first six hours to 14.5 per cent. According to these data four times as much of the penicillin treated in this way would have to be ingested on a fasting stomach instead of five times the dose in simple aqueous solution required over the intramuscular route. The method of preparation of the "modified" penicillin was essentially that of Welch *et al* (23) and the amount of the ingested dose recoverable in the urine was the same as they reported.

EXPT. 8. Chilling the stomach with large volumes of cold water simultaneously with the ingestion of the penicillin did not change the amount excreted in the urine.

EXPT. 9. This work was done to try to duplicate the findings of Little and Lumb (8) who reported that sodium bicarbonate in milk followed by penicillin dissolved in raw egg white resulted in urine levels of penicillin comparable to those following similar doses administered intramuscularly. Heatley (9) was unable to confirm this and obviously the data in Table I do not support it in the case of the subject used but show instead that the excretion was the same as would have occurred had the same dose been taken on a fasting stomach without the alkali and egg white.

EXPT. 10. This work was designed to see whether egg white alone would be as effective as with sodium bicarbonate and the data showed that this was the case. This suggests then that by giving penicillin with egg white it is unnecessary to keep the individual in the fasting state if five times as much penicillin is given as would be required by intramuscular injection instead of the use of thirteen times as much in the non-fasting state.

EXPT. 11. In order to test the protective action of egg white further, penicillin was given in an egg-nog containing the whites of three eggs on a non-fasting stomach. The total recovered in the urine was 8.2 per cent compared with 4.7 per cent in Expt. 12 where the same dose of penicillin was taken without egg white on a non-fasting stomach. This means that eight instead of thirteen times as much would be required to bring the urinary excretion levels up to the values attained by intramuscular injection.

Little and Lumb (8) attribute the protective action of egg white to its sulfur content. The acid buffering capacity of the egg white protein itself as well as its digestion products as they are gradually and continuously split off by the action of acid-pepsin might be important factors in the protective action.

EXPT. 12. Discussed under Expts. 3 and 11.

EXPT. 13. It is generally thought that gastric mucin elaborated by cells lining the stomach protect the mucosa from the action of the acid-pepsin. However, 25 grams of a concentrated mucin preparation swallowed and washed into the stomach with tap water followed ten minutes later by 100,000 units of penicillin in water was ineffective.

EXPT. 14. The buffering capacity of various substances with respect to 0.100 N HCl was determined as shown in Table II. It will be noted that only five grams of glycine prevented the pH from dropping below 3.1 when 150 ml. of the acid was added. Since previous experiments[6] had shown that penicillin was much more stable at pH 3.1 than would have been the case at the usual pH of gastric juice (about 1.8 or less), 20 grams of glycine dissolved in water was drunk on an overnight fasting stomach followed immediately by 100,000 units of penicillin in water. The resulting total urinary excretion was only 9.7 per cent.

EXPT. 15. Data in Table II show that acid is taken up by an activated carbon to a considerable degree. Since penicillin is readily absorbed by activated carbon it was decided to take penicillin orally with it to see whether the penicillin so absorbed would be protected from the action of the gastric juice with the thought that it might be eluted from the carbon for absorption in the duodenum and jejunum. Less than one per cent of the dose was recovered in the urine when five grams of Merck's activated carbon was used.

EXPT. 16. This experiment was undertaken to determine whether similar results could be obtained with the subject under study as those reported by Charney, *et al* (5). The data confirm their findings. When five grams of trisodium

[6]Unpublished data.

citrate were ingested on an overnight fasting stomach with 100,000 units of penicillin, 18.8 per cent of the dose was recovered in the urine. This is 30 per cent of the recovery after intramuscular administration and 166 per cent of the amount recoverable in the urine after ingestion under similar conditions except that no sodium citrate was taken simultaneously.

EXPT. 17. A heavy dose of ferric ammonium citrate proved to be of no advantage. It was taken with the thought of combining the oxidizing properties of the ferric iron with the acid buffering capacity of ammonium citrate. An oxidizing agent was used in an attempt to prevent the inactivation of penicillin in the strongly reducing medium of the upper intestine since Abraham and Chain (24) stated that penicillin was inactivated by such reducing agents as $NaHSO_3$ and $Na_2S_2O_4$ among others as well as by the primary alcohols and Cavillito and Bailey (25) and others (26, 27) reported that cysteine readily inactivated penicillin.

TABLE II

IN THE FOLLOWING EXPERIMENTS 5.0 GMS. OF EACH REAGENT WERE DISSOLVED OR SUSPENDED IN ABOUT 75 ML. OF DISTILLED WATER AND STIRRED VIGOROUSLY DURING THE ADDITION OF 0.100 N HCl WHILE NOTING CHANGES IN pH WITH A GLASS ELECTRODE

ml. 0.100 N HCl	Trisodium Citrate	Glycine	Egg Albumin Powder	Merck Activated Charcoal	Ammonium[1] Glutamate Solution	Ferric Ammonium Citrate	Di-ammonium Acid Citrate	Ammonium[2] Citrate Solution
	pH	pH	pH	pH	pH	pH	pH	pH
0	8.6	5.8	7.1	6.4	7.8	6.4	5.6	5.0
1	7.7	5.1	6.8	5.9	7.7	6.3	5.6	5.0
2	7.3	4.8	6.5	5.6	7.6	6.2	5.6	5.0
3	7.2	4.7	6.3	5.3	7.5	6.1	5.6	5.0
4	7.1	4.5	6.1	5.1	7.3	6.0	5.6	5.0
5	7.0	4.4	6.0	4.8	7.1	5.9	5.6	5.0
10	6.7	4.2	5.3	3.9	6.4	5.3	5.6	5.0
15	6.5	4.2	4.8	3.4	6.0	4.8	5.6	5.0
20	6.4	4.0	4.3	3.0	5.7	4.5	5.6	4.9
25	6.3	4.0	3.9	2.7	5.6	4.2	5.6	4.8
30	6.2	3.9	3.6	2.5	....	3.8	5.6	....
40	6.1	3.7	3.1	2.3	....	3.2	5.5	....
50	6.0	3.6	2.8	2.2	5.1	2.8	5.4	4.7
100	5.5	3.3	2.0	2.2	4.6	2.2	5.0	4.4
150	5.0	3.1	1.8	1.7	4.4	....	4.7	4.1
200	4.3	....	....	....	4.1	....	4.4	3.9
250	....	....	....	....	3.5	....	4.1	3.6
300	....	....	....	....	....	....	3.8	3.3

[1]5.0 gms. d-glutamic acid suspended in water, pH=3.3. Solution affected by addition of 5.5 ml. of concentrated NH_4OH. Final pH=7.8.

[2]3.3 ml. of a solution of 12 gm./fl. oz. of ammonium citrate kindly supplied by the Wm. S. Merrell Co.

EXPT. 18. Only an insignificant increase to 11.9 per cent excreted in the urine resulted from the simultaneous ingestion of ammonium glutamate over the 11.3 per cent recovery when the simple aqueous solution was drunk.

EXPT. 19. An elixir of ammonium citrate proved to be of no particular advantage in spite of its great *in vitro* buffering capacity as shown in Table II.

EXPT. 20. When five grams of diammonium acid citrate dissolved in water were drunk immediately following an aqueous solution of 100,000 units of penicillin on an overnight fasting stomach, only 6.6 per cent of the dose was excreted in the urine. This was only about one-third of the recovery resulting when the same amount of trisodium citrate was simultaneously ingested (compare with Expt. 16).

EXPT. 21. A heavy suspension of casein was found to have a protective capacity mid-way between that of powdered egg white and the non-fasting state (compare Expts. 10 and 12).

EXPT. 22. A heavy suspension of zein was tried because this protein is quite insoluble in water and it was felt that it might resist digestion in the stomach for some time and thus exert a protein acid-buffering protective capacity longer than in the case of soluble proteins. Compared with Expt. 10 it was found to be almost as efficacious as powered egg white.

URINARY EXCRETION AFTER INGESTION OF 43,250 UNITS WITH MAGNESIUM TRISILICATE AND OTHER ADJUVANTS

The penicillin used in compiling the data in Table III was in the form of tablets made up with magnesium trisilicate[7] to contain 4,325 units each. Ten of the tablets were taken by mouth for each of the experiments under the conditions described in the table.

TABLE III

URINARY EXCRETION OF PENICILLIN AFTER ORAL ADMINISTRATION OF 43,250 UNITS OF TABLETS MADE UP WITH MAGNESIUM TRISILICATE[1]

EXPT. NO.	DATE	CONDITIONS UNDER WHICH PENICILLIN WAS ADMINISTERED	PER CENT OF DOSE EXCRETED IN THE INTERVALS (HRS.)					TOTAL % OF DOSE RECOVERED
			0–1	1–2	2–3	3–4	4–6[2]	
101	1/31/45	With 300 ml. tap water on an overnight fasting stomach....	3.7	3.3	1.8	1.0	1.0	10.8
102	2/2/45	In tap water on an overnight fasting stomach followed immediately by 3 gms. U.S.P. sodium benzoate dissolved in tap water.....	1.1	2.3	1.1	0.6	0.4	.5
103	2/7/45	In tap water on an overnight fasting stomach followed immediately by 0.7 mg. atropine and 75 mg. phenobarbital.....	2.5	2.6	1.9	1.5	0.9	9.4
104	2/9/45	Same as No. 103 except the penicillin was taken 45 minutes after the atropine and phenobarbital were ingested..	1.9	3.2	.8	1.2	0.9	9.0
105	2/12/45	In tap water on an overnight fasting stomach followed by a suspension of 5 gms. of magnesium trisilicate in 350 ml. of tap water.....	1.2	2.5	0.9	0.3	0.2	5.1
106	2/14/45	In tap water on an overnight fasting stomach followed immediately by a suspension of 5 gms. of magnesium oxide in 400 ml. of tap water.....	0.9	0.6	0.1	0	0	1.6
107	2/16/45	In tap water on an overnight fasting stomach followed immediately by 5 Creamalin tablets (hydrous alumina) which had soaked overnight in water.....	3.6	2.9	1.3	0.6	0.4	8.8
108	2/24/45	With 1 pint of homogenized milk 1 hour after breakfast consisting of bacon, 1 egg, toast and butter, hot chocolate made with milk, and half grapefruit.....	0.2	1.0	1.0	0.4	0.5	3.1

[1]Kindly supplied by the Wm. S. Merrell Co.

[2]Regular lunch eaten in this interval.

EXPT. 101. 43,250 units were taken on an overnight fasting stomach. The 10.8 per cent total of the dose excreted in the urine compared closely with the amounts recoverable when 100,000 units were ingested (see discussion of Expts. 3 and 6). Obviously the incorporation of magnesium trisilicate with the penicillin in the tablet was not advantageous.

EXPT. 102. It is well known that the ingestion of sodium benzoate results in conjugation with glycine in the liver to form hippuric acid which is then excreted in the urine. Beyer et al (28) showed that the simultaneous intravenous administration of p-amino-hippuric acid with penicillin resulted in greatly prolonging the urinary excretion of the drug with attendant increased blood levels for long

[7]Obtained from the Wm. S. Merrell Co.

intervals of time. It was thought that the ingestion of sodium benzoate with penicillin might result in the delayed excretion of the latter because of preferential excretion by the kidneys of the hippuric acid formed in the liver from the sodium benzoate. Neither the total amount recoverable nor the rate of excretion data support the hypothesis.

EXPTS. 103 and 104. These data demonstrate that destruction by the gastric juice of penicillin taken orally was not significantly altered either by taking the drug simultaneously with atropine or by taking it after atropine at a sufficient interval for any maximal effect of the atropine on the secretion of gastric juice to have occurred.

EXPT. 105. These data show that the simultaneous ingestion of a large dose of magnesium trisilicate with penicillin had a deleterious effect on the amount of antibiotic activity recoverable in the urine. Possibly the magnesium trisilicate absorbed the penicillin and did not release it, or it may greatly prolong the emptying-time of the stomach similar to the view held by some concerning the action of sodium bicarbonate (13).

EXPT. 106. When five grams of magnesium oxide were taken as an antacid simultaneously with the tablets containing the penicillin, marked catharsis resulted. The data show that the penicillin may have been washed out of the stomach and intestine in the voluminous, watery stools. This was true both with respect to the total activity recoverable as well as the rate at which penicillin appeared in the urine. If the interpretation that the penicillin was washed out in the feces be valid, then the question arises as to whether the absorption from the gut into the blood stream normally may be only a slow process.

EXPT. 107. The results of this experiment are at variance with those of Expts. 7 and 23 in that hydrated alumina (Creamalin, Tablets) were not effective in preventing the destruction of penicillin taken orally under the conditions of the experiment.

EXPT. 108. Here the penicillin was taken about an hour after a meal and the data confirm the results of Expt. 12 (Table I). The recovery was only 3.1 per cent. When this is compared with the results of Expt. 101 it is seen that less than thirty per cent of the recovery when the drug was taken on a fasting stomach was obtained. These data mean that about twenty times the intramuscular dose would be required on a non-fasting stomach to bring the urinary excretion to the same level (compare with Expts. 3 and 11).

DISCUSSION

The data in these studies show that the maximal amount of oral penicillin recoverable in the urine was less than one-third of the antibiotic activity excreted in the urine after the same dose was injected intramuscularly. That this was true in spite of the simultaneous ingestion of large amounts of various antacids leads to the thought that gastric acidity is not solely responsible for the destruction of ingested penicillin. Rammelkamp and Helm (3) found that only 22.7 and 39.6 per cent of the ingested dose appeared in the urine of two achlorhydric pernicious anemia patients. Previous experiments[8] have shown that sixty-six per cent of the original activity was retained for twenty-four hours at 37° C. at pH 5 *in vitro*. In Table II it is seen that sufficient amounts of trisodium citrate and diammonium acid citrate were ingested with penicillin to have maintained this pH in the presence of 150 ml. and 100 ml. of one-tenth normal hydrochloric acid respectively. In spite of this similar *in vitro* buffering capacity, the data in Table I (Expts. 16 and 20) demonstrate that there was a three-fold difference in

[8]Unpublished data.

antibiotic activity in the urine. Since penicillin was taken with these buffers on a fasting stomach and was not followed by food, it is probable that little if any free hydrochloric acid was present or appeared soon after ingestion took place. Further, the bitter and nauseating concoctions probably would have inhibited gastric secretion for some time. Moreover, the data show that more than one-third of the total amount excreted appeared in the urine during the first hour when, according to the data of Bergeim (30), an average of only 0.07 per cent of free hydrochloric acid appears in the gastric contents during the first forty-five minutes after a meal.

It is thought that the decreased efficacy of oral penicillin, aside from that which does occur due to destruction previously by gastric acidity, may be due in large part to inactivation in the liver when the penicillin is absorbed into and carried by the portal system directly to that organ from the gastro-intestinal tract. The critical experiments of Florey et al (1) on this point merit repetition since their results were not conclusive in view of the small amounts of the drug which they had available for use in such experiments at that time. Recently Perlstein et al (20) presented evidence that the hypothesis could be correct and that the penicillin may be inactivated in the liver by coupling with glucuronic acid similar to the inactivation of aromatic acids, phenols and alcohols by conjugation with this acid (29). No suitable adjuvant which might prevent such conjugation is foreseen.

Conclusions and Summary

Bearing in mind all of the advantages and limitations imposed by the use of a single subject, the data presented in this report seem to justify the following conclusions with respect to that subject.

1. Five times as much penicillin is required to be ingested *on a fasting stomach* to give the same excretion of penicillin via the kidneys as by intramuscular injection in the subject used.

2. Thirteen to twenty times as much is required orally *in the non-fasting state.*

3. There is no difference between the penicillin extracted from surface cultures of the mold compared with submerged cultures with respect to destruction when taken orally as judged by recovery of antibiotic activity in the urine.

4. The same proportion of the antibiotic activity is recoverable in the urine when the same dose (based on antibiotic activity) of a very crude calcium salt of penicillin is ingested compared with a highly refined sodium salt of the drug.

5. There is no therapeutic advantage to the oral administration of penicillin suspended in cotton-seed oil over a simple aqueous solution of the drug.

6. Atropine taken simultaneously with oral penicillin or forty-five minutes before the antibiotic was ingested did not increase the proportion excreted in the urine over that recoverable when atropine was not taken.

7. Aluminum hydroxide taken with penicillin either did not change or increased only slightly (depending on the method of mixing) the amount of antibiotic activity recoverable in the urine. At best four times as much penicillin would have had to have been taken with the aluminum hydroxide on a fasting stomach to have given the same amount of excretion via the kidneys as by the intramuscular route of administration of penicillin.

8. Ferric ammonium citrate, ammonium glutamate, elixir of ammonium citrate, diammonium acid citrate, magnesium trisilicate, magnesium oxide, glycine, activated carbon, sodium benzoate, concentrated mucin, casein, and zein when ingested simultaneously with penicillin on a fasting stomach either decreased or did not alter the proportion of the antibiotic activity recoverable in the urine compared with oral administration in tap water.

9. The ingestion of five grams of trisodium citrate with penicillin increased the amount of the dose recoverable in the urine by sixty-six per cent over that recoverable without the salt but the amount in the urine was still only thirty per cent of that recoverable had the same dose been given intramuscularly.

10. Ingestion of penicillin with raw egg-white with or without sodium bicarbonate resulted in the same proportion of the penicillin being excreted in the urine as after taking the same dose with tap water on a fasting stomach.

11. Chilling the stomach with large volumes of cold water did not increase the amount of orally administered penicillin which appeared in the urine.

12. The capacity for the increased destruction of penicillin taken with food compared with oral administration in the fasting state persisted for several hours after the food was eaten.

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The Dice of Destiny

The Dice of Destiny is a timely book. These are days when some scientists must leave the ivory lab long enough to present in clear and simple language to the many the facts known to the few. Knowledge and good-will are both necessary if man is to control his destiny for the common good. Neither alone will suffice.

Dr. Rife, for many years a specialist in the field of human heredity, has made a notable contribution to a better understanding of human nature in this little book. He has chosen wisely in title, in content, and in method of presentation. The book is to be recommended as much for omission of subject material as for what is included. Without attempting to chart a course for the unsuspecting reader through the tortuous channels of modern genetics, the author has presented in compact form a wealth of pertinent facts on inherited variations as found in individuals, families, and races. He has dealt largely, though not exclusively, with genetic alternatives widely spread in human populations rather than with rare inherited abnormalities.

The first chapter begins with: "Take a piece of paper from the envelope on the back inside cover of the book, put it in your mouth and make a paper wad of it. Does it taste bitter?" This is perhaps the first time that an author has invited his reading public literally to taste a book. Even though that initial taste proves bitter, as it will to about 70% of readers, the reviewer will venture that few will stop until they have fed well on the substantial meal which follows.

A concise discussion of the inheritance of taste, blood groups, hair, skin and eye color, sex and sex-linked characters, twinning, finger-prints, handedness, mental capacity, and special abilities is included. Racial variations in these and other traits are considered. A sound presentation of the relative roles of heredity and environment, of eugenic methods and their probable results, and of racial and individual variations, gives the reader a background for understanding the problems of human nature. In the closing chapter, "Genes and Democracy," current fallacies about race are exposed, a glimpse of possible scientific advances leading to improved environment is given, and an equality of opportunity for all is urged.

Unfortunately the book, otherwise attractive in format, is marred by frequent typographical errors. It is to be hoped that these will be corrected in a second printing, as some of them will prove confusing to the general reader.—*Warren P. Spencer.*

The Dice of Destiny, An Introduction to Heredity and Racial Variations, by David C. Rife. 163 pages, 23 figures and 14 tables. Long's College Book Co., Columbus, Ohio, 1945. $1.75.

STUDIES IN LABORATORY REARING OF ANOPHELES QUADRIMACULATUS SAY[1]

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Since a constant supply of healthy, vigorous, adult mosquitoes was needed for use in various studies being made on insect repellents, laboratory rearing of *Aedes aegypti* and *Anopheles quadrimaculatus* was initiated. No difficulties were encountered in rearing *Aedes* but the same cannot be said for *Anopheles*, consequently this paper deals only with the latter species.

A generous supply of *Anopheles quadrimaculatus* eggs was obtained from the U. S. Department of Agriculture, Bureau of Entomology Laboratory at Orlando, Florida, in November, 1943. The method of rearing followed at that time was obtained from notes made by Dr. C. E. Venard at Orlando and from the publication by Crowell (1940). In following these methods certain difficulties were encountered in rearing the larvae through the four instars. It was learned that other laboratories were having similar rearing troubles. This paper is written to report several modifications of the above mentioned techniques with the hope that the suggestions offered will be of value to those now engaged in similar work and helpful to those who may later become interested in such activity.

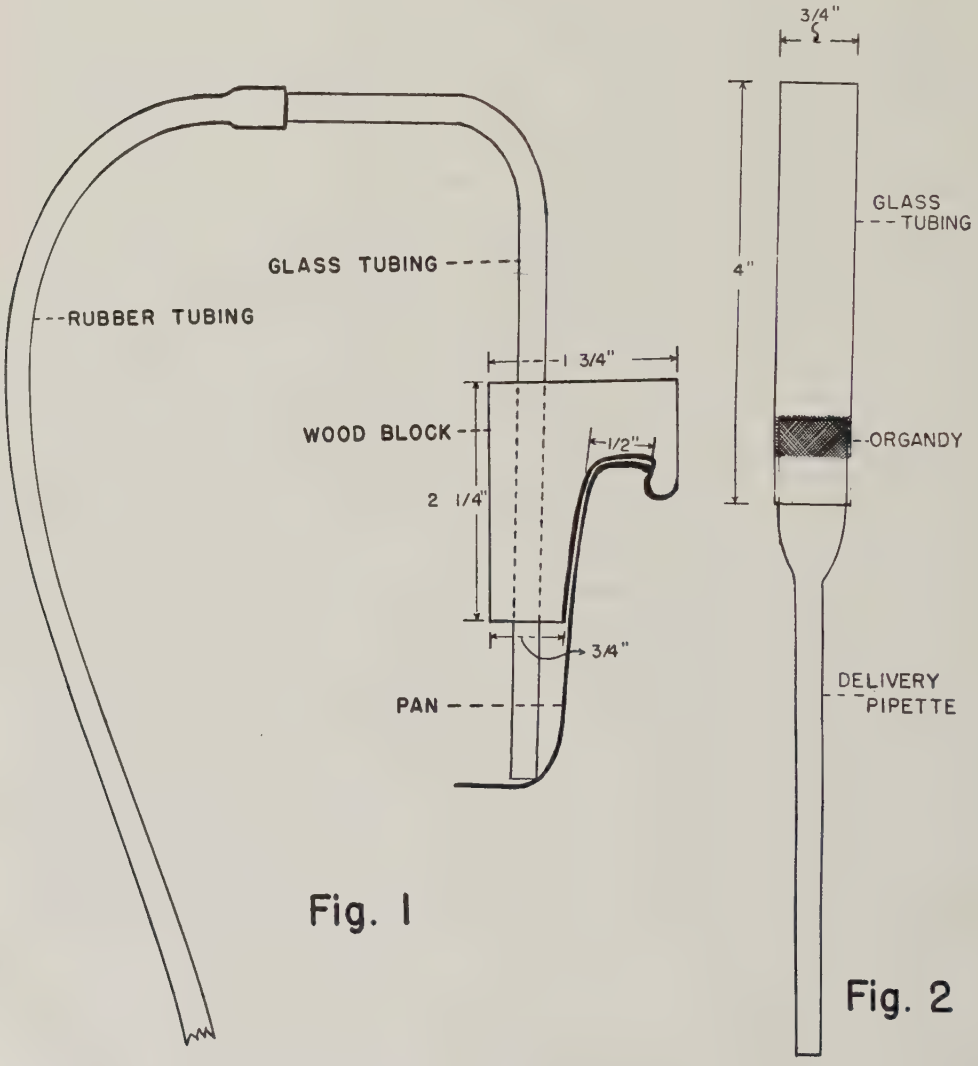
The rearing room was 11 x 6½ feet with a ceiling 10 feet high and lighted by a fluorescent lamp containing two 40-watt white tubes, which was on only during the day. The temperature was maintained at approximately 80° F. and the relative humidity varied from 40 to 70 per cent, but most of the time it was very near 50 per cent.

ADULTS.—The adults for egg-laying were maintained in a 16 mesh screened thirty-inch cubical sleeve cage. Water was available to the mosquitoes in the oviposition pan. As a source of food each cage was supplied daily with a piece of absorbent cotton approximately one inch square saturated with a 5 per cent honey solution in water and in addition a blood meal was furnished by allowing them to feed from the clipped belly of an immobilized rabbit introduced into the cage for one-half hour. The rack for holding the rabbit was similar to that used by Campbell, Barnhart and Hutzel (1941) with the exception that the bottom, sides and ends were completely enclosed. This eliminated all hiding places and very few mosquitoes escaped into the room when the apparatus was removed from the cage. Another precaution taken to prevent escape was the use of a rubber tube from a compressed air line to blow the mosquitoes off the rack and away from the sleeve as the rabbit was being withdrawn. It was found that the rabbit lay more quietly if its head was not exposed to the mosquitoes in the cage, consequently the sleeve of the cage was pinned around the neck and the head remained outside.

The population was maintained by placing jars containing pupae in the stock cage. A screen wire cone with 1½ inch opening at the top was placed over each jar to allow the emerging adults to escape into the cage, but prevent egg-laying adults from ovipositing in them. On alternate days a 5″ x 5″ cylindrical screen wire cage with a 1″ x 4″ opening and a sliding celluloid lid was placed over a jar where emergence was underway and the adults thus obtained were placed on a shelf to give a series of cages of "dated" mosquitoes for use in laboratory tests.

[1]The work described in this paper was done under a contract recommended by The Committee on Medical Research, between The Office of Scientific Research and Development and the Ohio State University Research Foundation.

Eggs.—For oviposition a white enameled pan 10 inches in diameter and $2\frac{3}{4}$ inches deep containing water to a depth of 1 to 2 inches was placed in the stock cage daily. On the following day it was removed and all adults picked from the surface with a pair of forceps. The water was siphoned off by means of a device made from a block of wood $\frac{3}{4}''$ in thickness, and a glass tube with dimensions as shown in Figure 1. The pan was set on a gently sloping surface so that the water



Figs. 1 and 2. Devices for concentrating Anopheline eggs.

would run to the lower side. The flow from the siphon was stopped just as the floating eggs near the outlet were about to be carried off in the stream of water. The eggs were left on the sides and bottom of the pan. They were then washed into a 100 ml. beaker by means of a wash bottle, and the contents poured slowly into a funnel sieve. Care should be exercised especially when large batches of eggs

have been collected as they may partially block the passage of water and rapid pouring may result in an overflow. The funnel sieve shown in Figure 2 may be held in position by a burette clamp on a ring stand or held in the hand while the eggs are being washed from the beaker. It consisted of a glass tube four inches in length, open at both ends, the outside diameter of which was three-fourths inch and large enough to allow the top half of a 10 ml. delivery pipette with the end covered with two thicknesses of a fine mesh organdy to fit snugly inside. After the eggs had been washed into the funnel, the delivery pipette was pushed upward through the open tube and the organdy removed.

The eggs were placed in an enameled pan 10 inches in diameter to hatch. The pan was filled with water to a depth of 1½ to 2 inches. A paraffined cardboard ring, 3½″ o.d. and 2¼″ i.d. was floated in the water. This was used to prevent the eggs from floating to the edge of the pan and adhering to the sides following evaporation of the water. The organdy covered with eggs was then placed on the

TABLE I

A Comparison of Rate of Larval Development in Shallow versus Deep Water

Number Days After Hatching	Number Pupae Collected	
	Shallow Water	Deep Water
10	2	0
11	14	0
12	38	0
13	34	5
14	51	24
15	50	53
16	32	45
17	18	52
18	5	51
19	0	11
20	0	6
21	0	2
Total Pupae	250	250
Larval Mortality	7	22
Percentage Mortality	2.7	8.5

surface of the water inside the ring. The eggs floated off and the cloth sank to the bottom and was carefully removed with a pair of forceps. Two days after the eggs had been "set," hatching occurred. Several counts of the total number of larvae hatching from one day's supply revealed than from 3,000 to 10,000 eggs were deposited.

Larvae.—Following hatching 250 larvae were counted into each of two oblong Pyrex dishes (No. 232) containing approximately 150 ml. of water. The number of larvae could be determined quickly and accurately by the use of an ordinary medicine dropper and a Veeder hand tally or counter. Groups of recently hatched larvae were sucked up in the medicine dropper and as they were slowly forced out into the water in the dish the number was recorded on the counter in the other hand. A white background was necessary in order to see the larvae easily. No further manipulation was required until pupation occurred.

The Pyrex dishes were selected because they were a standard product generally available, they had a flat bottom and were uniformly rectangular in shape which made possible efficient use of shelf space. They were 12 inches long, 8 inches wide and 2 inches high.

Depth of water was determined by a study of larval development in shallow and deep water. Two Pyrex dishes (No. 232) were used in the test, each containing approximately 250 larvae. Water depth in one was maintained at one-eighth inch which required 150 ml. of water, and in the other at one-half inch, requiring 600 ml. of water. The quantity of powdered food supplied each dish was the same. Repeated tests gave results similar to those shown in Table I.

These data show that the larvae in the shallow water developed more rapidly than those in deep water and with less mortality. This may be due to the fact that larvae in the shallow water swept the bottom with their mouth brushes and obtained the food that settled. They can do this with their respiratory plates remaining at the surface. The water was clear with no scum, and very few organisms such as bacteria or protozoa could be found indicating that they were unnecessary for proper larval development. The pupae from the deep water dish were smaller in size indicating inadequate food supply. Additional food added to the deep water dish to compensate for that which the larvae could not reach

TABLE II

A Comparison of Rates of Development of Larvae Using Dog Food and Yeast in Different Proportions

Number Days After Hatching	Number Pupae Collected Daily		
	Dog Food and Yeast, Equal Parts	Dog Food—1 part Yeast —2 parts	Dog Food—2 parts Yeast —1 part
9	9	1	1
10	59	21	15
11	93	91	81
12	67	88	82
13	14	28	53
14	1	8	11
15	0	1	1
Total Pupae	243	238	244
Mortality	7	5	9
Percentage Mortality	2.6%	2.05%	3.56%

because of settling, resulted in scum formation, a considerable amount of gelatinous, flaky, suspended material and murky water. Microscopic examination of the water from such dishes revealed a very high population of bacteria, principally *Escherichia coli* and protozoa of the genera *Oikomonas*, *Hartmanella*, and *Colpoda* as determined by Professor W. J. Kostir and Dr. C. E. Venard. All these protozoa are air borne forms and primarily bacteria feeders. Once a dish became clouded or murky, death of most of the larvae was certain and if held for further development, a few larvae usually reached the pupal stage but the rate of development was greatly retarded. Results indicated that when this occurred it was best to dispose of the contents of the entire dish. An over-abundance of food, especially in the earlier instars increased the number of cloudy dishes.

A logical explanation for the greater mortality in the deep water dishes seemed to be that the excess food resulted in an abundance of bacteria, which appeared to be an ideal medium for protozoa because they increased greatly in numbers. The bacteria, being anaerobic, deoxygenated the water and along with the excess of food, a scum was produced on the surface that interfered with the dissolving of oxygen of the air into the water. The scum also clogged the respiratory plate

of the larvae causing them to struggle to free the plugged area, resulting in many of them being trapped in the flaky, gelatinous suspended material.

The larvae were fed *twice daily* with a mixture of equal parts by weight of finely ground[2] Purina dog food and powdered dried brewer's yeast. This mixture was tried in other proportions for effects on development and the results are shown in Table II. Peak pupation was reached more quickly when equal parts of dog food and yeast were used and mortality was greatest when dog food predominated and lowest when yeast predominated.

Studies were made on the amount of food required for each instar and the results are presented in Table III. Because all the larvae did not molt at the same time a safe range on quantity of food was given for the third and fourth instars which were the periods of greatest growth and food consumption. With practice an approximation of these amounts could be administered by means of tapping a salt shaker containing the food mixture a given number of times. Just as the food landed on the clear and ambered colored water, the small particles scattered rapidly over the entire surface. It was noted that this surface tension reaction did not take place in the dishes where the water was clouded.

TABLE III

Quantities of Food for Each Instar Required Twice Daily for 250 Larvae

	Milligrams of Food per Dish of 250 Larvae, Fed Twice Daily			
	Instars			
	1	2	3	4
1. Slow Growth Low Mortality Water Clear	10	20	50	75
2. Normal Growth Low Mortality Water Clear	20	30	60–80	80–90
3. Normal Growth High Mortality Water murky plus scum and suspended flaky food material	30	40	90	100

Before the shallow water technique was proven to be superior to that of using deep water, a study was made of the possibility of changing the physical properties of the food so that it would float on the surface for several hours. After numerous trials this was accomplished by thoroughly mixing 160 175 ml. of water with a mixture of 50 grams of powdered dried brewer's yeast and 50 grams of finely ground dog food using an electric kitchen mixing machine. A teaspoonful of the resulting paste was then placed in the center of one-half of a sheet of waxed paper 6 x 12 inches. The other half of the paper was folded over the mixture and pressed between two panes of glass. This quantity of food mixture made a very thin layer six inches in diameter when treated in this way. When all of the food mixture had been pressed, the halves of the papers were separated and allowed to dry, after which they were crumpled to remove the flakes of food. These were broken up

[2]Laboratory model "Micropulverizer" with Herring bone Screen No. 035H B. S1.

so as to pass through 30 mesh screen, but in breaking them up some fine particles were produced and these were removed by sifting through an 80 mesh screen.

A check was then made on the relative merits of flaked versus powdered food in deep and shallow water. Two Pyrex trays were filled with 150 ml. of water and two with 600 ml. of water. Into each tray was then counted 255 larvae. The trays were fed once daily the same quantity of food. The results are given in Table IV. Repeated tests gave similar results.

TABLE IV

A Comparison of Rate of Development and Mortality in Shallow and Deep Water Using Flaked and Powdered Food

Number Days After Hatching	Number Pupae Collected			
	Powdered		Flaked	
	Shallow	Deep	Shallow	Deep
10	.....	.....	.....	.....
11	42	7	30	12
12	125	56	89	48
13	65	82	84	75
14	1	18	42	59
15	.....	13	8	36
16	.....	4	1	15
17	.....	1	.....	3
Total pupae	233	181	254	248
Percentage Mortality	8.6%	29.0%	0.39%	2.7%

The results indicate that when powdered food was used the shallow water technique was superior to that of using deep water. Where flaked food was used very little difference in mortality resulted. The pupae from the deep water trays receiving powdered food were noticeably smaller. Since making flaked food is an additional chore its use is not recommended even though in this test it gave slightly lower mortality than powdered food in the shallow water trays.

Pupae.—The pupae were removed daily by means of a wide mouth medicine dropper and placed in four to six inches of fresh tap water in jars six inches in diameter. Jars this size will accommodate 600–800 pupae. Following removal of pupae the larvae from the last two or three dishes were combined into one dish to conserve space. The above described technique produced a daily average for the 7½ month period from December 1, 1944, to July 22, 1945, of 490 pupae with 94.8 per cent emergence and peak pupation in from 10 to 13 days after hatching.

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CHERMES ALNI, TWO CENTURIES AFTER KALM (HOMOPTERA: PSYLLIIDAE)[1]

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Apparently the definition of *Chermes alni* Linnaeus and the limitations imposed by the definition in the tenth edition of Systema Naturae, page 454, 1758, have either been ignored or not thoroughly investigated and the definition in Fauna Suecica, page 263, 1761, has been considered the original description; thus the entire concept of *Chermes alni* has been taken from this latter work. In his "Tenth Edition" Linnaeus states, "*Habitant in Betulae Alni ramulis Larvae, caudis plumosis tectae, in* America *septentrionali. Kalm.*" There is nothing in the International Rules of Zoological Nomenclature that invalidates this description. Since Peter Kalm is cited as collector of the insect under discussion any ecological data furnished by Kalm is certainly valuable and can not be discounted because of acquisition prior to 1758. An insect must be collected before it can be described and any data, whether pinned on the same pin as the specimen or not, should accompany the specimen. It is of further interest to note while Linnaeus' description of *alni* in the tenth edition has been ignored for purposes of original description, the North American record as taken from that work has been carried through the years and has recently resulted in *Psylla alni americana* Crawford being placed as a synonym of typical *alni* on the grounds that since *alni* was described from America *americana* must represent this form.[2] It should be noted in this connection that the American form described by Crawford as *americana* is known only from the far West. Had Kalm's notes been consulted it is not likely that this action would have been taken.

The English version of 1770, of Peter Kalm's travels in North America revised from the original Swedish and edited by Adolph B. Benson, on page 81, reads, "Chermes on the alder (*Chermes alni*)[3] were today found in great abundance on the branches of that tree, which for that reason looked almost white and at a distance appeared as if it were covered with mould." This account appears under Kalm's entry of October 3, 1748, on the journey to Wilmington, Delaware, from a farm near Philadelphia, Pennsylvania. These data with the original description furnish enough information to identify the insect as the only species covered with white flocculent material occurring in dense masses on the branches of alder in late fall in the vicinity of Philadelphia, Pa. On October 7, 1945, I was able to collect from alder immediately north and east of Philadelphia, and on October 12, 1945, I collected from alder immediately south and west of that city. Not one specimen of Psylliidae was taken from alder. Anyone contending that Kalm observed a species of Psylliidae has yet to report the occurrence under conditions described by Kalm of such an insect from Eastern North America to say nothing of the Philadelphia area. The topotypic insect found in such numbers as to make the alder branches appear covered with mould has been identified by the Bureau of Entomology and Plant Quarantine, Division of Insect Identification, as *Prociphilus tessellatus* (Fitch); therefore I am convinced that Kalm observed the insect known as *Prociphilus tessellatus* (Fitch) and that this species is a direct synonym of *Chermes alni* Linnaeus.

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[1]An elucidation of the facts for authority to use the family name Psylliidae instead of Psyllidae or Chermidae. (See: Jr. N. Y. Ent. Soc. 52: 335, 1944.)

[2]Tuthill, L. D., Iowa State College Jr. Sci. 17: 460–461, 1943.

[3]The original reads, "*Chermes alni Linnei* Faun. Suec. 698." (See: En Resa til Norra America 2: 276, 1756.)

Since *alni* belongs in the Aphioidea and is the type species of the type genus *Psylla*, the family name goes with the zoological concept into the aphids. The next available type designation, which will maintain the zoological concept, is Kirkaldy's *Psyllia*, type *pyri* (L.) making the family name Psylliidae. Kirkaldy's type designation is definite and valid under the "Code" regardless of the reasons upon which he based his decisions. By admittance of these facts the old controversy of Chermidae vs. Psyllidae, which arose from Geoffroy's noncommittal treatment of a composite group that resulted in differences of opinion as to his intent, is legitimately and logically bypassed. There is no need to submit the question of Chermidae vs. Psyllidae to the International Commission for an opinion. Those who wish to preserve either name as a "*nomina conservanda*" must now submit a name based upon an interpretation of Geoffroy's intent as opposed to a name acceptable from both a zoological and nomenclatural viewpoint.

A NEW SPECIES OF TILLUS FROM ARIZONA (COLEOPTERA: CLERIDAE)

JOSEF N. KNULL,
The Ohio State University[1]

Tillus patagoniae n. sp.

Male.—Somewhat resembling *Tillus collaris* Spin. in size, color and shape. Head, prothorax, scutellum, and last two visible ventral segments of abdomen reddish brown; elytra black; abdomen, antennae, and legs dark brown, tarsi lighter.

Head convex; surface finely densely punctured, light pubescence short; labrum entire; eyes emarginate, finely granulate; antennae with eleven segments, extending to basal fourth of elytra, segments five to ten inclusive serrate, slightly longer than wide.

Pronotum longer than wide, wider at apex than at base, widest in middle; sides sinuate; disc convex, with transverse depression near base and on anterior fourth; surface finely, densely punctured, light pubescence about same length as on head. Scutellum small.

Elytra much wider than widest part of pronotum, widest on apical third; sides subparallel near base, expanded back of middle, apices broadly rounded to suture; disc convex; surface with coarse punctures arranged in rows, separated by less than their own diameters, interspaces narrower than punctures, not visibly punctate, light pubescence short, dense.

Abdomen beneath shining, minutely punctured, pubescence sparse. All five tarsal segments visible from above.

Length 4 mm.; width 1.6 mm.

Female.—Last three visible ventral segments of abdomen reddish brown.

Variations.—Some specimens have the head dark, basal segments of antennae and abdomen lighter brown.

Described from specimens collected in the Patagonia Mountains, Arizona, on July 23, by D. J. & J. N. Knull. Male holotype, allotype and paratypes in writer's collection. Paratype in collection of The Ohio State University.

This species has shorter, wider elytra than *T. collaris* Spin. Elytral punctures are smaller and short, dense, light pubescence gives the elytra a gray appearance.

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[1]Contribution from Department of Zoology and Entomology.

A PHYLOGENETIC STUDY OF THE FERNS OF BURMA

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I. Introduction[2]

The purpose of this study is to arrange the ferns of Burma in the most natural system possible according to observed patterns of variation within the fern group.[3] This goal cannot be fully achieved at present because of the very inadequate paleontological record and the very incomplete knowledge of the morphological, anatomical, physiological, and chemical characters of both sporophyte and gametophyte generations of the genera and species involved. As Carl Christensen (1938) has pointed out, many important features observed in a single or few related species are not yet known to be characteristic of all species of the same genus; as a matter of fact hardly one character ascribed to a genus is to be found in all its species! Phylogenetic systems of classification of ferns to date should be recognized as provisional attempts to fit together and integrate the growing evidence available from all sources and to record tentative conclusions as to relationship.

The interpretation of data is a prime factor in the building of any phylogenetic system, for the seriation of individuals and groups depends upon the phylogenist's concept of progression. Phylogeny is in disrepute in some quarters (Bremekamp, 1942) because of the wide difference in interpretation of the same data. Since validity of the system rests upon the validity of the interpretation, it is essential that the principles of interpretation be clearly stated. It may well be that some of the elaborate taxonomic structures we have built are—like every other building—only structures. The quicker such fabrications are recognized and demolished, the quicker we will get to that final goal, a natural classification.

PHYLOGENETIC CONCEPTS AND THEIR MEASUREMENT

Somehow or other the present forms of life have arisen from fewer forms. Phylogenists attempt to systematize these organisms according to their true relationships. Inasmuch as some of the bases for such systems are of doubtful validity, a consideration of the concepts involved will be of value.

It is often taken for granted that recent ferns are more advanced than ancient ones, but this is not necessarily so. Eames (1936) states that some of the oldest

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[1]Papers from the Department of Botany, The Ohio State University, Columbus 10, Ohio, No. 490.

[2]This paper represents part of a dissertation accepted by the Graduate School for the doctorate degree from the Ohio State University.

[3]My thanks are due to Dr. R. R. Stewart, Head of the Botany Department of Gordon College, Rawalpindi, India, for his continued encouragement, his aid in preliminary identification, and for his loan of Burma specimens after my Rangoon collection was in the hands of the Japanese; to the late Dr. Carl Christensen for his identification of my specimens of *Dryopteris* and *Polystichum;* to the late Dr. John H. Schaffner for his clearcut teaching on phylogenetic taxonomy; to the Chicago Museum of Natural History for the loan of the fern specimens collected by the Cutting Sikkim Expedition of the Field Museum; to the Rev. Harold Young for permission to study and name his fern collection made along the Stilwell Road on the Assam-Burma border; to the Arnold Arboretum for financial assistance in collecting in Burma; to Prof. C. A. Weatherby for making available the facilities of Gray Herbarium; to Dr. W. R. Maxon for his aid in identification and his kindness in making available the facilities of the U. S. National Herbarium; and to Dr. Lois Lampe and Dr. E. N. Transeau of Ohio State University for their reading of this manuscript and their helpful suggestions.

known forms of the Psilophytales are the most complex of that group suggesting that there must have been a long antecedent period of evolution. Campbell (1940) has pointed out that the Cycadofilicales may be considered as either the most advanced of the ferns or the most primitive of the gymnosperms. They are geologically ancient but definitely advanced in the possession of heterospory and seeds; they themselves were derived over a long preceding period from other and more primitive ferns. Had they survived to the present day, they would no doubt have been considered more advanced than our living ferns; the fact that very few of them survived the paleozoic period (Seward, 1931) in no way cancels out their advanced characteristics. Ancient ferns are not necessarily archetypic: the terms *ancient* and *recent* are not, therefore, to be used indiscriminately for *primitive* and advanced.

Bateson (1915) raises the question whether we are limited to the old view that evolutionary progress is from the simple to the complex, and whether, after all, it is conceivable that the progress was the other way about. Eames (1936) takes the position that some cases of simplicity are primitive and that others, due to reduction, are advanced. But can primitive simplicity be distinguished from simplicity due to reduction? Is *Monogramma dareicarpa* Hk. which Benedict (1919) claimed to be the simplest fern in existence, also the most primitive? Is the simplicity of the Hymenophyllaceae due to reduction as believed by Copeland (1938), or is it hereditarily simple? Such questions cannot be readily settled by appeal to the morphology of apparently simple organs; rather the complexity of the reaction system responsible for the organ must be studied. The complexity of the system is to be judged by the complexity of potentiality in the protoplast rather than by apparent complexity due to size or to a great multiplication or repetition of similar parts. (Schaffner, 1934.) Monogramma's one linear sorus located asymmetrically on a small leaf does not therefore indicate primitive simplicity.

Bower (1923), Copeland (1907, 1929a), and others have repeatedly judged those forms to be the most advanced whose structures seemed to have developed the most "biological advantage" by natural selection. As a matter of fact the degree of survival value of an organ is the second of the two touchstones used by Bower to determine which end of his phyletic series is to be considered primitive and which advanced. But as Cain (1944) has so clearly pointed out, although apparent biological advantage, gained through supposed adaptation of structure, is often superficially credible, yet it is never safe to reason from the structure to the function, as adaptation does not necessarily reside in the obvious but is rather the result of hereditary change. Care must therefore be exercised not to confuse apparent biological advantage with advance.

If phylogenetic advance cannot be measured directly by geologic age, nor by the degree of supposed biological advantage gained through selection, nor unerringly by the superficial complexity of organs, by what means can it be estimated?

First, different levels in the plant kingdom have been rather generally recognized by botanists, but these levels have been most clearly defined by Schaffner (1934, 1938, 1939). He carefully listed the fundamental potentialities of the reaction systems of the plants at ten different levels, and has shown that the majority of homosporous leptosporangiate ferns have 60 of these general potentialities, and the heterosporous ferns 69 to 70. These fundamental characters which determine the general level of ferns in the plant kingdom and, to a certain extent, within their own phylum, will be considered more fully in the section on the ground-plan of ferns.

To determine the relative position of any given fern within the phylum, one may catalog all the special characteristics which a species manifests throughout its life cycle in addition to the character-accumulation for the entire phylum to which it belongs, thus securing a list of the total potentialities or characteristics possessed

by that species. By this method Schaffner has shown *Ophioglossum vulgatum* L. to possess a total of 95 potentialities as against 105 for *Onoclea sensibilis* L. and 122 for *Marsilea quadrifolia* L. By such lists of the total character complex, the relative level or degree of advance of a species may be ascertained if the study of the various species is made on the same general basis. A simple listing of characters, without an attempt at evaluation, eliminates the possibility of arbitrariness in establishing relative values. The fact of accumulation of characters with resulting complexity should be a guiding principle in phylogenetic taxonomy.

One weakness in the use of the total character complex mentioned above would seem to be that all characters are considered to be of equal value in determining the degree of advance: a potentiality for reticulate venation is given equal weight with that for dichotomous venation; the potentiality for a well developed annulus counts no more than that for a vestigeal one. Therefore an additional way to determine the relative position of a fern within the phylum is to evaluate the morphological characters and functional activities as to their general or specialized nature. A thorough study of fern genera and species shows certain patterns of variation occurring repeatedly in different lines. In these phyletic series the more specialized forms are considered to be the more advanced. A detailed evaluation of the characters of leptosporangiate ferns will be found in a later section of this paper.

TYPES OF EVIDENCE ON WHICH A PHYLOGENETIC STUDY OF FERNS MAY BE BASED

Were it possible, a direct reconstruction of the historic development of ferns from fossil remains would give the most certain phylogenetic arrangement, for a complete record of the past, if properly interpreted, would establish the proper sequence of the taxonomic series. Unfortunately the fossil record is, and always will be, very fragmentary. Only a fraction of the kinds of ferns of the past have been preserved in fossil form, and of these only a fraction are recognizable specifically. Seward (1931) agrees that we cannot expect to discover a solution to the problem of evolution from the records of the rocks, though he does think that these fragmentary relics of the past enable us *to make tentative guesses* at the truth. Reference to such scattered and fragmentary fossil records as the chief method of determining which end of a phyletic series is primitive (Bower, 1923) is of doubtful validity. Whether the modifications in the various phyletic lines appeared in the historical order of the phyletic series, we have, in most cases, no direct way of checking; but as these variations have all appeared in the genetic complex, seriation from primitive to advanced is justifiable.

A second type of evidence frequently used in phyletic study is that from ontogeny. Bower (1923) holds that ontogeny reflects the probable phylogeny. But even though there may be a marked change in the structure and distribution of tissues or in the form of organs during the development of the individual, there seems to be little justification for claiming that the structure during the juvenile stage is more primitive than that of the adult stage just because the former precedes the latter. Both juvenile and adult forms are the expression of the same genetic complex. Such changes seem to be associated rather with changes in size of organs, patterns of growth, and physiological gradients. Phylogenetic variation may or may not run parallel with the changes occurring during ontogeny. It is an entirely different matter, and quite right, to consider the potentialities expressed throughout the life-cycle as a basis for the comparison of forms.

A third type of evidence valuable in phylogenetic taxonomy is the chemistry, whereby plants may be classified according to the substances made by them. By contrasting the protein precipitation reactions of a large number of ferns Mez (1925), Conradi (1926), Wilkoewitz (1929), and other workers have attempted

to establish the natural relationships of these plants. A diagram showing the conclusions of Mez is given by Gortner (1938). Chester (1937) has reviewed the results of this type of work and concludes that so many factors influence the strength of serological reactions that their value is chiefly qualitative rather than quantitative. This fact, together with the rather widely varying results obtained by the workers in the Konigsberg and Berlin schools, definitely limits the serological approach to the interpretation of plant relationship. It is probable, however, that this method might contribute information if techniques were better standardized, and if more species were tested. At present, so far as ferns are concerned, the results may be considered as suggestive only.

McNair (1932, 1934, 1935, 1945) has attempted to use a different type of chemical evidence on which to base relationships. He maintains that the higher the relative molecular weights of the plant alkaloids, the more unsaturated the fats, the higher the specific gravities of the volatile oils and the lower their refractive indices, the more advanced the plant or plant group. Although he has not dealt with the ferns, his method would be applicable to them. One serious weakness of his theory is that the chemical values which he uses vary rather markedly in the same plant when grown in different environmental conditions.. For instance, the iodine number of linseed oil varies from 175–210. With such a range of variation any indicated relationship would, of necessity, be very indefinite. Results for plants grown in the same controlled environment might be significant. Another weakness is that the range of iodine values is greater within the single order Ranales, 31–129, than in most of the other angiospermic families put together. Since this is true, what value can there be in the comparative averages for the large groups with which he works?

Other chemical evidence such as that supplied by color reactions of lignin (Crocker, 1921) may ultimately prove of value in phylogenetic taxonomy.

A fourth kind of evidence is that derived from genetics and cytology (Cain, 1944). Gregory (1941), McKelvey and Sax (1933), Foster (1933), Whitaker (1933), Cleland (1936), and others have applied such evidence to good effect in clearing up the systematics of certain angiospermic groups. For example, it has been shown that polyploidy has been very important in developing large, complex, and widespread angiospermic genera. The genetic analysis of ferns, however, has only just begun (Anderson-Kötto, 1938), and thus far very little use of results has been made. That such use will bring worthwhile results is shown by the study made by Conley (1944) in which she shows that *Nephrolepis exaltata* and some of its varieties fall into three groups with chromosome numbers 76±, 57±, and 28±.

A fifth type of evidence, and most important in this study, is that derived from the physiology, morphology, and life-cycle of living ferns. Since the beginning of the century it has become more widely accepted that since ferns lack flowers—structures on which the taxonomy and phylogeny of the angiosperms is almost entirely based—any natural taxonomic arrangement of ferns must be based on the very broad foundation of the morphological and physiological characteristics of all organs of the plant during its development. This at once makes the study of fern relationship much more difficult not only because the basis of comparison is wider but also because evidence derived from different organs may not be readily harmonized. We are lead to the conclusion that all organs do not progress phyletically at equal rates; one organ or part may have advanced decidedly while another remained stationary (Bower, 1923, Schaffner, 1934). Despite this inequality of advance of different organs of the same fern, the ideal of phylogenetic taxonomy is to base the system on the sum of all available evidence.

Bower, in his invaluable work, The Ferns (1923, 1926, 1929) established twelve criteria of comparison by the use of which he tried to work out the true relationship of ferns. They are:

1) The external morphology of the shoot.
2) The initial constitution of the plant body as indicated by meristematic segmentation.
3) The architecture and venation of the leaf.
4) The vascular system of the shoot.
5) The dermal appendages.
6) The position and structure of the sorus.
7) The indusial appendages.
8) The characteristics of the sporangium and spores.
9) The spore numbers.
10) The morphology of the prothallus.
11) The position and structure of the sexual organs.
12) The embryology of the sporophyte with special reference to the suspensor.

In the present state of our knowledge some of these criteria such as Nos. 2, 10, 11, 12, and to some extent No. 9, seem to be of importance in distinguishing the eusporangiate from leptosporangiate ferns. Inasmuch as the leptosporangiates differ from the eusporangiates in so many fundamental ways that they seem unlikely to have been derived from the fully evolved eusporangiate ferns, this study will confine itself to those criteria deemed valuable in the study of the leptosporangiate ferns.

Smith (1938) in his summary of developments within the fern group makes no reference to Bower's Nos. 2 and 5. Eames (1926) believes that No. 12 has no real value for comparison. But if Bower includes some criteria which are not particularly useful in this study, he also overlooks some. To his criteria should certainly be added:

13) The development and differentiation of sporophylls.
14) The time of sex-determination in the life-cycle.

It will be noted that these fourteen criteria are, in the main, morphological in nature. Our very limited knowledge of the physiology, and of growth and differentiation, forces us to express our conclusions at present largely in morphological terms, but ultimately when it becomes possible to speak in terms of patterns of growth, the present rather confused picture of such things as leaf type, architecture, and venation may be cleared up (Foster, 1936).

From this survey of evidence available for use in a phylogenetic study of the ferns, it would seem that very heavy reliance must still be placed on the morphological life history, though the physiology, chemistry, and genetics of ferns may prove to be of increasing value in years to come.

II. A Review of the Schemes of Classification Proposed Since the Beginning of the Century

The usual practice in the past in the segregation of families has been to put all ferns with a more or less complete vertical annulus into the family Polypodiaceae, thus including in one family ⅞ of all living ferns. The other ⅛ have been, without much difficulty, separated by marked segregative characteristics of annulus and vegetative form into about 15 other very natural and often isolated families by such men as Robert Brown, Martius, Kaulfuss, John Smith, Presl, and Bower. These are composed of such similar and easily recognized forms that there is more or less general agreement as to their treatment. The real phylogenetic problem, therefore, rests not with them but with that great residual group of about 7,000 species which have been lumped together on the basis of one character, the more or less vertical annulus. It is with them that we shall deal in this review. For an excellent survey of the earlier treatment of these ferns, reference may be made to John Smith's *Historia Filicum* (1875).

Diels (1902) divided the "Polypodiaceae" into 9 tribes, 6 of which were subdivided into 2 subtribes each, and 1 into 4 subtribes. Christensen (1906) arranges the Polypodiaceae according to Diels' outline without change. Bower (1928) makes 11 tribes which are based directly on the tribes and subtribes of Diels, with the one exception that he breaks up Diels' No. IX, Acrosticheae, inserting most of the acrostichoid species under other tribes as acrostichoid derivatives. Copeland (1929) gives numbers rather than names to his divisions of the family which he enlarges to include such genera as *Plagiogyria*, *Cyathea*, *Dicksonia*, *Cibotium*, and *Matonia* in order to preserve the Polypodiaceae as one phylogenetic unit (a procedure which is not likely to stand). He disagrees with Diels and Bower as to the relationship of many separate genera, but there is a more or less close correspondence of his groups with theirs, as shown in Chart I.

CHART I

A Comparison of the Sections of Copeland and Diels

Note: The first digit of Copeland's numbers indicates the phyletic line, and successive figures branches of these lines.

Copeland	Diels
121–123	I. Woodsieae
124	II. Aspidieae
1252	V. Asplenieae Blechninae
1253	V. Asplenieae Aspleniinae
241 and 32	IV. Davallieae
242	VI. Pterideae
30	III. Oleandreae
421 and 422	VIII. Polypodieae, Section 1
423–426	VIII. Polypodieae, Section 2
51–54	VII. Vittarieae

Christensen, in his *Third Supplement* to the *Index Filicum* (1934) again, follows Diels' order but makes changes here and there which bring his system closer to Copeland's. Christensen clearly states that this is only a partial revision as he was preparing a thorough one to appear four years later in the *Manual of Pteridology* (1938). In that, his final and most complete revision, he divides the old comprehensive, Polypodiaceae into 15 subfamilies which, he says, might better be considered as families. Christensen does not follow Diels in placing the annual water fern, *Ceratopteris*, in a family by itself; rather he makes it a tribe in his subfamily VI, the Gymnogrammeoideae. Nor does he follow Bower in placing *Dipteris* in a separate family, instead, making it his subfamily XIII, the Dipteroideae. Also he separates the Lindsayoid ferns from the Davallioid, putting them into his subfamily II, the Lindsayoideae. In other respects his groups correspond very closely with the tribes and subtribes of Diels and Bower, as may be seen by reference to Chart II.

CHART II

Comparison of the Treatment of the Polypodiaceae by Christensen, Bower, and Diels

Note: The roman numeral before each group refers to its original position in the list to which it belongs. The arabic numerals refer to the subsections of the larger groups.

Christensen	Bower	Diels
I. Dennstaedtioideae	I. Dennstaedtiinae	IV. Davallieae In part
II. Lindsayoideae	II. Davallioid ferns Section 3	IV. Davallieae In part
III. Davallioideae	II. Davallioid ferns Sections 1 and 2	IV. Davallieae In part
IV. Oleandroideae	II. Davallioid ferns Of uncertain place	III. Oleandreae
V. Pteroideae	III. Pteroid ferns	VI. Pterideae 4. Pteridinae
VI. Gymnogrammeoideae 1. Cryptogrammeae 2. Ceratopterideae 2. Gymnogrammeae 4. Adianteae 5. Cheilantheae	IV. Gymnogrammeoid ferns 1. Primitive genera 1. Primitive genera 2. Central group 3. Adantoid ferns 4. Cheilanthoid ferns	VI. Pterideae 2. Cheilanthinae (Parkeriaceae) 1. Gymnogramminae 3. Adiantinae 2. Cheilanthinae
VII. Vittarioideae	XI. Vittarioid ferns	VII. Vittarieae
VIII. Onocleoideae	VII. Onocleoid ferns	I. Woodsieae 2. Onocleinae
IX. Blechnoideae	VIII. Blechnoid ferns Sections 1, 2 and 3	V. Asplenieae 2. Blechninae
X. Asplenicideae	VIII. Blechnoid ferns Section 4 VI. Asplenioid ferns	V. Asplenieae 1. Aspleninae 1. Aspleninae
XI. Woodsioideae	V. Dryopteroid ferns 1. Woodsieae	I. Woodsieae 1. Woodsiinae
XII. Dryopteroideae	V. Dryopteroid ferns 2. Aspidieae	II. Aspidieae 1. Aspidiinae
XIII. Dipteroideae	(Dipteridaceae)	II. Aspidieae 2. Dipteridinae
XIV. Polypodioideae	IX. Dipteroid derivatives	VIII. Polypodieae IX. Acrosticheae 2. Platyceriinae
XV. Elaphoglossoideae	X. Metaxyoid ferns Section 2	IX. Acrosticheae 1. Acrostichinae

The most adventurous treatment of the old group, "Polypodiaceae" is that by R. C. Ching, *On the Natural Classification of the Family "Polypodiaceae"* (1940), in which he divides the 170 or so genera with a more or less vertical annulus into 33 families, 21 of which closely parallel Christensen's subfamilies and tribes, the other 12 being segregates of one or several genera from groups where they did not seem to be closely related. It may be questioned whether anything is gained by treating

such groups as families rather than subfamilies and tribes, but in any case Ching seems to have done the logical thing in breaking up into natural families the old "Polypodiaceae," if that group be truly polyphyletic as Bower and Christensen believe. In most cases he has defined natural groups and established order by increasing the number of subdivisions of the Filicales; in this way the number of units per group decreases, and they may be more easily surveyed. See Chart III.

CHART III

COMPARISON OF THE TREATMENT OF "POLYPODIACEAE" BY CHING AND CHRISTENSEN

NOTE: The dots indicate side branches from the main series.

Ching	*Christensen*
LINDSAYOID-DAVALLIOID SERIES	
1. Culcitaceae Ching	Dicksoniaceae—Dicksonioideae (part) (or in I. Dennstaedtioideae)
2. Dennstaedtiaceae Ching	I. Dennstaedtioideae—Dennstaedtieae
Dennstaedtieae	Chaetopterides
Saccolomeae	Lepidopterides
3. Lindsayaceae Ching	II. Lindsayoideae
Lindsayaeae	
Taenitideae	
Stenolomeae	
4. Dictyoxiphiaceae Ching	II. Lindsayoideae (1 genus)
5. Davalliaceae Gaud.	III. Davallioideae
Davallioideae	
Nephrolepioideae	
6. Oleandraceae Ching	IV. Oleandroideae
PTEROID-GYMNOGRAMMEOID SERIES	
7. Hypolepidaceae Ching	I. Dennstaedtioideae—Hypolepideae
8. Pteridaceae Ching	V. Pteridoideae
Lonchitideae	Chaetopterides
Pterideae	Lepidopterides
9. Sinopteridaceae Koidzuma	VI. Gymnogrammeoideae (part)
Onychieae	Cryptogrammeae (a)
Allosoreae	Cryptogrammeae (b)
Cheilantheae	Cheilantheae
10. Gymnogrammaceae Ching	VI. Gymnogrammeoideae (part)
Gymnogrammeae	Gymnogrammeae—Chaetopterides
Gymnopterideae	Gymnogrammeae—Lepidopterides
11. Adiantaceae Presl.	VI. Gymnogrammeoideae(part)
	Adianteae
. . . . .	
12. Ceratopteridaceae C. Chr.	VI. Gymnogrammeoideae (part)
	Ceratopterideae
. . . . .	
13. Antrophyaceae Ching	VII. Vittarioideae
	Part of B
14. Vittariaceae Presl., emend.	VII. Vittarioideae
Monogrammeae	Part A
Vittareae	Part of B
15. Loxogrammaceae Ching	XIV. Polypodioideae (1 genus)
THELYPTEROID-ASPLENIOID SERIES	
16. Aspleniaceae Presl.	X. Asplenioideae
Asplenieae	Asplenieae
Athyrieae	Athyrieae
17. Thelypteridaceae Ching	XII. Dryopteridoideae (part)
Thelypterideae	Thelypterideae (1st part)
Goniopterideae	Thelypterideae (2nd part)
Dictyoclineae	Dryopterideae (Sect. of Tectaria)
18. Sphaerostephanaceae Ching	XII. Dryopteridoideae (part)
	Thelypterideae (1 genus)
19. Monachosoraceae Ching	XII. Dryopteroideae (part)
	Thelypterideae (2 genera)
. . . . .	
20. Blechnaceae Ching	IX. Blechnoideae
Blechneae	
Woodwardieae	
Braineae	

CHART III—(*Continued*)

Ching	*Christensen*
CYATHEOID-ASPIDIOID SERIES	
21. Onocleaceae Ching	VIII. Onocleoideae
22. Woodsiaceae Ching	XI. Woodsioideae
23. Hypoderriaceae Ching	Between XI and XII
24. Perenemaceae Presl., emend.	Between XI and XII
25. Aspidiaceae Presl., emend.	XII. Dryopteroideae
Dryopterideae	Dryopterideae (Nos. 1–18)
Aspideae	Dryopterideae (Nos. 19–37)
26. Didymochlaenaceae Ching	XII. Dryopteroideae
	Dryopterideae (1 species)
27. Acrostichaceae Presl., emend.	V. Pteridoideae (derivatives)
DIPTEROID-POLYPODIOID SERIES	
28. Cheiropleuriaceae Nakai	XIV. Polypodioideae
	Chaetopterides, 1 genus
29. Dipteridaceae Bower	XIII. Dipteridoideae
30. Platyceriaceae Ching	XIV. Polypodioideae
	Chaetopterides, 1 genus
31. Polypodiaceae Presl. (sensu propria)	XIV. Polypodioideae—Lepidopterides
Pleopeltoideae	Pleopeltideae
Lepisoreae	Nos. 4–10
Phymatodeae	Nos. 11–36
Polypodioideae	Polypodieae
Polypodieae	Nos. 37–40
Campyloneureae	No. 41
32. Grammitaceae Presl., emend.	XIV. Polypodioideae—Lepidopterides
Grammitieae	Polypodieae Nos. 42–48
Cochlidieae	Polypodieae Nos. 49–51
33. Elaphoglossaceae Ching	XV. Elaphoglossoideae

Unfortunately from the point of view of phylogeny, Ching is, on the whole, very dogmatic in his segregations, in very few cases giving adequate discussion or sufficient explanation of the bases for his divisions, and nowhere stating any principles by which he interprets his data. However, Ching worked with Carl Christensen for several years and followed his ideas very closely, so that, in a sense, Ching carried the work of Christensen to a logical conclusion. Christensen here and there states the principles on which he builds his system, but he nowhere draws them together in a unified statement. As a matter of fact no fern taxonomist has adequately presented the principles upon which he has based his phylogenetic disposition of species. True, here and there statements are made which help us to understand the points of view, but these tend to be scattered and incomplete. The morphologists have been less hesitant in trying to formulate principles of progression; certain it is that a statement of principles is essential if these are to be accurately understood and assessed.

III. The Ground-Plan of Ferns

If we are to arrange the ferns in series from the primitive to the more advanced, it is essential to have a starting place. Different workers vary widely in their conception of the theoretical primitive type. Bower (1935) pictures it as follows: "Such an *archetype sporophyte* would have consisted of a simple upright shoot of radial symmetry, probably rootless, dichotomising if it branched at all, and with the distinction between leaf and axis either absent or ill-defined. The leaf, where recognizable as such, would have been long stalked, with distal dichotomy, tending in advanced forms towards the sympodial development of a dichopodium. All the limbs of the dichotomy would be narrow and distinct from one another. The

whole plant would be relatively robust as regards cellular construction, generally photosynthetic, and traversed by conducting strands with a solid xylem-core. The surface would be glabrous, or invested with simple enations. The solitary sporangia would be relatively large, and distal in position, with thick walls, and a simple method of dehiscence; and each would contain numerous homosporous spores." Bower carefully states that he is not implying that the Psilophytales represent the direct ancestry of the Filicales, but if the above description of the supposed primitive fern type implies anything, it is just that. Campbell (1940) says that there is some evidence that the Filicineae may have been derived from some of the Devonian Psilophyta but that it is problematical. He pictures the primitive sporophyte as consisting of a single leaf and a "protocorm" or foot, with the root presumably being of later development. Eames (1936) comments on the proposed primitive type by saying, "The Psilophytales are indeed 'ancient and simple;' that they are also 'archaic and ancestral' is not surely known."

Though the relationship of the ferns and the Psilophyta is problematical and unproven, Bower and his followers do base their ideas of progression and development directly on that assumption, even to the cladode nature of the megaphyll or fern leaf. The present writer believes that so long as the actual origin of the ferns is so uncertain, it is unwise to start with an assumption which, if untrue, would invalidate the whole phylogenetic structure built upon it.

Must we than conclude with Seward (1931) that the theoretical primitive type eludes our grasp; that though our faith postulates its existence, yet that type has failed to materialize? Fortunately there is an alternative far safer than to base our type on a very problematical ancestry, and far more positive than to make no effort at all. A generalized ground-plan can be drawn for the ferns by placing together those fundamental potentialities of the phylum to which they belong (Schaffner, 1934) but which appear for the first time in the plant kingdom as we know it in the ferns. Such a generalized type for the homosporous ferns would show the following characteristics: it would have a 2-phased sporophyte with a parasitic embryonic stage and a later completely independent stage. The sporophyte would have either an unbranched or a branched stem with long-continued, indeterminate apical growth. The stem tip would display either negative or transverse geotropism; the well developed vascular system would be composed of xylem and phloem. On the stem in a spiral pattern would be typical leaves with a vascular supply; these would be decidedly dorsiventral, usually with phototropic reactions when young. In most lines they would have a circinate vernation. Sporangia producing spores of one kind would be borne on the leaves. Spore formation would not be followed by the immediate death of the sporophyte except where the potentiality for continued growth were inhibited by the introduction of the annual habit as in *Ceratopteris*.

This is the ground-plan for all homosporous ferns; to get to the heterosporous ferns there would have to be added to this character complex the fundamental potentiality which causes a shift in the time of sex-determination from the ontogeny of the gametophyte back to the sporophyte, resulting in heterospory and highly dimorphic unisexual gametophytes which are also much reduced, short-lived, and dependent on the parent sporophyte for their food supply.

The above description is made up of the fundamental characteristics of all the ferns. It is, therefore, a generalized picture which is as true for primitive as for advanced forms. Since it is impossible, as Seward has intimated, to postulate with any certainty the theoretical primitive type for the ferns, this ground-plan which must have been true for the primitive type also, is the next best approach. We have than a starting place for our study, not theoretical and postulated, but actual. The evolution of the ferns has consisted in the variation of expression of this ground-plan at every point and in any number of different ways.

IV. The Phyletic Patterns of Variation of the Leptosporangiate Ferns

A taxonomist trained to work with specific and generic plant types and precise descriptions of plant organs and structures is often at a loss to know how to harmonize his concepts with those of the newer morphology of the last two decades (Watson, 1943) whose trend has been away from fixed categories and static concepts of structural and specific entities towards a more dynamic and fluid condition. The terms *leaf* and *stem* have become for some no more than convenient descriptive words without biological meaning (Arbor, 1930). The species is "a momentary realization of a line of evolution (Faegri, 1935). Concepts which describe form are being replaced by concepts dealing with the regulation of growth (Schüepp, 1933). However, as Watson (1943) points out, although the nature of the descriptive terms or units employed be changed, yet units of some kind are indispensable for all description. By building on the most fully substantiated morphological concepts of the past until they are actually replaced by something nearer the truth, and at the same time making use of new facts available from all sources, the taxonomist can approach with confidence a study of the phyletic patterns of variation among the ferns.

1. Posture. As often happens in phylogeny, experts may disagree in their interpretations: whereas Bower (1923) holds the erect stem to be the more primitive type, Eames (1936) says that the rhizome type appears primitive for the group. Copeland (1938) believes that at least for the Hymenophyllaceae the creeping rhizome is primitive and the ascending or erect stem derived.

The pose of the adult stem is not determined by its orientation in the embryo but rather by the direction of growth of the young stem. Stems may be upright from the first by continued growth of an erect embryo as in *Angiopteris* if the stem be negatively geotropic; but if, as in the case of *Helminthostachys*, it be transversely geotropic, then it quickly grows to a prone position. In the majority of the leptosporangiates where the embryonic stem is lateral and prone, the growth of the young stem is negatively geotropic and by continued growth becomes erect as in *Cyathea* and *Brainea*, or suberect as in *Polystichum*. If, however, the young stem displays transverse geotropism, it will continue to grow in a prone position. The negatively geotropic growth of erect stems with radial symmetry would seem by analogy with other vascular plants to be the more fundamental; horizontal growth with its various and frequent change of symmetry, the more specialized and derived. Ferns having both erect stems and runners or rhizomes as in *Matteuccia struthiopteris* Tod., in *Nephrolepis cordifolia*, and in some species of the Cyatheaceae are considered here to be more advanced in this respect than related forms with only a single stem type.

2. Other specialized forms of stems. Those specialized forms of stems such as the tuberous stems of *Nephrolepis cordifolia* and *Todea barbata*, the inflated and hollow (sometimes ant-inhabited) stem of *Myrmecophila*, the climbing stems of *Stenochlaena* and *Lomagramma*, the runners with distinct nodes and internodes of *Marsilea*, and the rhizophores of *Oleandra neriiformis* are considered as derived and advanced, not because of any degree of supposed biological advantage associated with the structure, but because some very real new potentialities have been added to a primitive ground plan complex. They should not be thought of as "adaptations"—past, present, or future!

3. Rate of growth. The rate of growth varies from very slow as in most erect stems and some prostrate ones, to very rapid as in ferns like *Marsilea* and *Lomagramma*. Judging by comparison with the eusporangiate ferns and the Cycadophyta the slow growth associated with upright stems would seem to be the relatively more primitive condition. It is also associated with a more complex phyllotaxy which in a later section is considered to be a primitive characteristic.

Secondary growth due to a vascular cambium must also represent an added protoplasmic potentiality.

4. Branching of stem. The upright fern stem is normally unbranched though apical twinning sometimes takes place, involving presumably the equal division of the apical meristem. In no upright fern stems known to the writer is there repeated and regular dichotomous branching, and Wardlaw (1943b) points out that what Bower considered in many ferns to be delayed branches of unequal dichotomy probably have a different origin. Dobbie (1929, 1930) tells of a forest of forked tree ferns in New Zealand, but he attributes such branching to adventitious buds rather than to dichotomy. Wardlaw (1943 a and b) gives very interesting evidence to show that the branches of the erect stems of *Matteuccia struthiopteris* which form horizontal rhizomes can be traced to "detached meristems" to be found always in proximity to regions of meristele conjunction. His investigations with other ferns such as *Dryopteris aristata* and *Onoclea sensibilis* suggest that buds on fern stems near leaf bases are not adventitious; their position is regular and fixed in relation to the meristele conjunctions, that is axillary in origin though often moved out of the axil by growth distortion.

Prostrate stems may be unbranched, may branch by dichotomy as in *Pteridium aquilinum* and *Onoclea sensibilis*, by axillary buds as in the Hymenophyllaceae, *Marsilea*, and *Leptochilus axillaris* (Cav.) Kaulf., or by buds not distinctly in the axils of leaves as in *Onoclea sensibilis* which Wardlaw has shown to be of probable axillary origin. It would seem that branching due to buds associated with leaf bases represents a potentiality added to the unbranched or dichotomously branched condition. If branching by both dichotomy and axillary buds is present as in *Onoclea*, two heritable factors for branching must be present and consequently the hereditary reaction system of the plant may be considered more complex.

5. Stele. Bower places great emphasis on the comparative value of the stele type, concluding that "the vascular tissues provide the most constant character of the plant body." Van Tieghem's stelar theory (1886) has furnished material for much phylogenetic discussion. It has been held by Gwynne Vaughan (1901), Bower (1923), Eames (1936), Smith (1938), and Campball (1940) that the protostele is primitive and that the siphonostele and dictyostele are successively more advanced. One hesitates to take a position which differs from that of such an impressive group of authorities, but their position needs to be carefully reconsidered in the light of recent research. The evidence for their belief is based on the fact that some of the Gleicheniaceae and Schizaeaceae, and the Hymenophyllaceae, which are for other reasons regarded as ancient and primitive, possess a protostele in their adult stems. Among ferns with a polypodioid type of sporangium protostely may be found in *Cheiropleuria* and the tribe Monogrammeae of the family Vittariaceae.

Let us examine this evidence to see if it is sufficient to warrant the conclusion that protostely is the primitive condition. First, not all of the species of the Gleicheniaceae are protostelic, one section of the family having solenosteles. The same may be said, and more emphatically, for the Schizacaceae, because of the four genera of that tribe only one, *Schizaea*, is protostelic: *Lygodium* is solenostelic, and *Anemia* and *Mohria* are dictyostelic. If protostely is the primitive condition, certainly it is not very well fixed, for other types of steles seem to be more common than protostely in these presumably primitive families. And what about the Hymenophyllaceae in which protostely is rather more universal? Copeland (1938) believes that reduction is the key to an understanding of the family. If this is true, protostely in the family may be the result of reduction and therefore not a primitive characteristic.

Certainly evidence from these supposedly primitive families is not very convincing, particularly when added to it is the fact that protostely never occurs in

the adult stems of other supposedly primitive fern families and genera. The Ophioglossaceae have solenosteles or dictyosteles, while the Marattiaceae and Angiopteridaceae have what Bower (1926) called "undoubtedly the most complex vascular system of all living Pteridophyta," a polycylic dictyostele. The Osmundaceae have dictyosteles, and the Matonaceae have "one of the most complicated solenostelic structures among ferns," a polycyclic solenostele with three concentric rings of vascular tissue. Certainly the evidence from living ferns supposedly primitive is very unconvincing. If one bases his judgment on the living evidence, the decision would have to be otherwise.

The second type of evidence which has lead to the conclusion that the protostele is more primitive than the solenostele, and the latter more primitive than the dictyostele, comes from the ontogeny of the fern plant. A young sporeling usually has a protostele, but in all except the few genera named above where the adult stem retains the protostelic structure, as the stem grows and increases in diameter upward, the stele develops into a siphonostele or solenostele, and sometimes into a dictostele. By taking the events of ontogeny as a pattern for phylogeny the case for the primitive nature of the protostele is established to the satisfaction of some.

Just what is involved in the change from protostele to dictyostele? In the course of individual development the simple protostele may become medulated, a condition which leads to solenostely, and this, in turn, in shoots where the foliar gaps overlap, to dictyostely. Wardlaw (1944a) has pointed out that the condition of the fully differentiated tissues in the basal portion of the young stem where protostely exists is primarily referable to the size, activity, and nutritional status of the apical meristem at the time of inception of that stage; and similarly for the fully developed tissues in the higher region where a solenostele is formed. He also shows (1944b) that the leaf gaps in the shoot stele do not form if leaf primordia are destroyed at a sufficiently early stage, and that the solenostele which would have become a dictyostele due to overlapping of leaf gaps, remains a solenostele. Therefore, the condition of the differentiated tissues in the upper, normally dictyostelic level of the stem is referable not only to the size, activity, and nutritional status of the apex at the time of the inception of that stage, but also to the modifying influence of developing leaves. He thus demonstrates very clearly that there is no phylogenetic difference between a solenostele and a dictyostele, and little or none between a protostele and solenostele.

The increasing size of the apical meristem, then, plays a definite part in the shift from protostely to solenostely, but not from solenostely to dictyostely which is controlled by leaf development. It should be pointed out, however, that there are a few cases of "perforated" dictyostele, as in leafless tubers of *Nephrolepis cordifolia* (Sahni, 1916), where increasing size of the organ appears to be of importance in determining the internal morphology.

What then can be concluded about the occurrence of stele types and their phylogenetic significance? Dictyostely is normally associated with erect and suberect stems, and with decumbent stems which are relatively thick and whose leaves are close and many ranked so that the leaf gaps overlap. Siphonosteles are normally associated with prostrate stems of smaller diameter having leaves few ranked and (or) so far apart that the gaps do not overlap. Protostely in fern stems is usually associated with prostrate stems of small diameter. If the large erect stem with many-ranked leaves is primitive, and the decumbent stem with few-ranked leaves is derivative, then in that sense the dictyostele may be considered more primitive than the solenostele and protostele. But since the stele type is so closely associated with the stem size, stem posture, and leaf arrangement, it would seem that these characters have been far more important phylogenetically than the stele type. In this discussion, therefore, little value will be attached to it.

6. Epidermal outgrowths of the shoot. Christensen (1911) says that

the best and most constant specific character is to be found in the dermal appendages, hairs and scales. These appendages may vary within a species, in abundance but not in kind. They may be remarkably constant for a whole genus as in *Pyrrhosia*, or extremely variable as in *Asplenium*.

Some genera such as *Microlepia* may possess hairs only, while others such as *Cyathea* may have some species with hairs and some with scales; *Histiopteris* may have both hairs and scales on the same shoot. Families such as the Osmundaceae includes genera which are all characterized by hairs only, while others such as the Oleandraceae have scales only on their stems but may have hairs on their leaves. Such families as the Schizaeaceae, Gleicheniaceae, Cyatheaceae, Gymnopteridaceae, and Thelypteridaceae have both hairs and scales occurring in their genera or sections. It is clear then that though the kind of dermal appendage may be constant within a species, it is not necessarily so in larger groups. Since both hairs and scales are present in such supposedly primitive families as the Gleicheniaceae and Schizaeaceae, it is apparent that hairs and scales are not very fundamentally different, and their presence, though of specific value, may not be of great phylogenetic significance.

The simple hair is the product of a simpler growth process than a branched or stellate one, or than a scale. Hairs vary from one- to many-celled, and from unbranched to branched. Scales vary in shape, size, color, point of attachment, thickness of walls, and margin; it seems impossible to trace any one pattern of variation for all scales. A few generalizations, however, may be made: a scale with a basal point of attachment may be more easily derived from a hair than one with a broad base or one peltately attached. Clathrate scales having thick cell walls and clear lumen seem more specialized than those with smaller undifferentiated cells without clear lumen. Scales with entire margins may be simpler than those with dentate or ciliate margins. A glabrous shoot may be thought of as more primitive than one having a potentiality for the development of dermal outgrowths; care must be taken, however, not to mistake an adult shoot from which the outgrowths have dropped or been rubbed off for a truly glabrous one.

Before considering patterns of variation of the fern leaf it will be well to examine briefly the recent thought concerning the nature of the leaf. It may be summed up thus (Bower, 1935): the megaphyll, or leaf of the ferns proper, is of cladode nature, i. e., it is a modified branch system having its origin in the dichotomous branching of a stem not yet fully differentiated as axis and appendage. Since the leaf is supposed to be only a stem, primitive leaves would be highly branched, the various branches being green and not webbed together. Although Bower has based his phyletic series on this hypothesis, he was not satisfied that it represented ultimate truth as may be seen by a statement of his (1938) in the introduction of Verdoorn's Manual of Pteridology: "Certainly the last word . . . on the origin of leaves . . . has not yet been spoken." We agree with this opinion.

Not only is the actual origin of fern leaves still quite uncertain, but leptosporangiate fern leaves differ in some very fundamental ways from all known branch systems in their circinate vernation during the growing period of the leaf, their direct spiral arrangement on the stem, the sporadic or regular presence of buds in their axils, and the reticulate venation of the leaves of many species. The distinctness of the leaf and stem, often from the quadrant stage of the embryo, is a strong argument that the leaf is not simply one limb of a dichotomously branched stem. Since the origin of the fern leaf is not really known, and since it differs in these fundamental ways from known branch systems, in this study the older morphological concept of the leaf as an organ distinct in nature from the stem and root will be maintained. What is primitive in the patterns of variation will not be decided on the assumption that the psilophytan branch system is the prototype of the leaf, but upon other criteria.

7. Phyllotaxy. As Schaffner has so well shown in his paper on the Spiral Systems in Vascular Plants (1938a) there is a general progression from the complicated multispiral leaf arrangement to the alternate 2-ranked condition, and in a very few cases to the 1-ranked condition. His generalizations hold for the ferns, those with relatively large erect or suberect stems and dictyosteles having many-ranked leaves as is also the case in some decumbent stems with dictyosteles, for example, *Pteridium aquilinum*. In many decumbent stems, particularly in those with a siphonostele or protostele the leaves are two-ranked (or in some cases possibly one-ranked). Rarely leaves are whorled as in *Salvinia* where three leaves occur at each node, and as in some species of the Cyatheaceae where whorls of 3, 4, 5, and 6 leaves are known. In whorled types 3 or more leaves develop almost simultaneously. As has been pointed out above, the phyllotaxy is always correlated with the stele type, and both are correlated with the stem type or posture.

8. Articulation of the petiole to the stem and abscission. John Smith (1875) held the articulation of the petiole to the stem to be a character of such prime importance that he used it together with a phyllotaxis character to found his primary section Eremobrya. The present writer cannot follow Smith in making articulation a framework character for the segregation of ferns into large primary groups, but it is a specific or generic character. Very frequently articulation, together with abscission, is associated with an epiphytic habit as in *Oleandra*, *Davallia*, and some of the Polypodiaceae *sensu strictu*. That it is in no sense limited to epiphytes can be seen from its occurrence in *Cyathea*, *Angiopteris*, *Elpahoglossum*, and a few species of *Asplenium*. Articulation is a character which would have to be added to the ground-plan complex, and its presence is therefore to be considered an advanced character.

9. Articulation of pinnae or pinnules to rachis or rachilla. John Smith (1875) did not include in his section Eremobrya those ferns lacking articulation at the base of the petiole even if their pinnae were articulated to the rachis. Such articulation, very frequently resulting in abscission on drying, is present in *Nephrolepis*, *Drynaria*, *Lomagramma*, *Stenochlaena*, *Dicymochlaena*, *Angiopteris*, *Woodsia* Sect., *Physematium*, and in some species of *Adiantum* and *Lygodium*. Such articulation may or may not be associated with an epiphytic habit, although the first two genera mentioned above have many epiphytic species. The succeeding genera and species mentioned are typical terrestrial ferns, so that it would be inaccurate to conclude with Copeland (1907) that articulation arises as an adaptation to the epiphytic habit, and to habitats where ferns must sometimes endure a more or less prolonged drought. Were this true, we might expect articulation and abscission to be present in all epiphytes and in most terrestrial ferns of monsoon regions, where the rainfall is seasonal, but this is not the case.

Such articulation may characterize whole genera as *Drynaria* or only certain species in a genus as in *Lygodium*. Its occurrence in the ferns as a whole does not seem to form a pattern or to parallel any one or more phyletic lines, but rather appears here and there as a marked character. Its presence indicates the addition of a new factor to the ground-plan complex; ferns having articulation are to be considered that much more complex in their development than those which lack it.

10. Leaf traces. The number and arrangement of the meristeles, or vascular bundles, in the petiole base at the point of union with the stem is a diagnostic character of importance which is easily ascertained in fresh material. This information should be recorded in the description of all species; at present generalizations are difficult because this is one of those characters which Christensen might have had in mind when he said that many important characters known to exist in some species of a genus are not yet known to occur in all. However, Waters (1903) has used this character on which to base a key to the ferns, and Ching (1940) in his key to the 33 families which he segregated from the old

family "Polypodiaceae," divides them into two groups, the first having one leaf trace, and the second, two or more traces. Unfortunately there are always exceptions which make unsatisfactory the use of this character with as large groups as families.

Wardlaw (1944b) shows that in young petiole bases the procambial strands are uninterrupted and crescent-shaped, made up of small-celled tissue which during growth fails to keep pace with the enlargement of the pith within; hence the vascular crescent becomes disrupted into five to seven or more separate strands or traces. If, however, the further growth of the primordium is inhibited or prevented at an early stage, the normal enlargement of the pith does not take place and the crescentic mass of primordial vascular tissue remains coherent or disrupted only to a limited extent. It is possible that what Wardlaw has found to be true for *Dryopteris* spp. may also hold for other ferns in which the leaf trace or traces are arranged in the form of a horseshoe, trough, or V. It would seem then that the pattern of variation of leaf-traces in ferns with dictyosteles is from the continuous shapes just mentioned to the interrupted C or V, the individual meristeles of which may be either elongated or rounded. In ferns with decumbent or climbing stems, distant leaves, and protostele or solenostele, the petiole bases usually have one trace either round or V-shaped,—rarely split into two traces. There is no such irregular arrangement of traces at the petiole base as that shown for *Pteridium aquilinum* by Waters (1903).

11. Degree of dissection of the blade. It should be recalled that in this study the fern leaf is treated as an organ *sui generis* and not as of cladode origin. Should the megaphyll sometime be really proved to be a modified branch system, this section and certain others concerning the leaf would have to be completely revised. Bower (1923) and all those who like him establish their ideas of the fern leaf on the very problematical psilophytan ancestry of the ferns hold that the large highly divided leaf is more primitive than a smaller simple leaf; that the simple or less divided forms have arisen from the more divided by the webbing of branches. This is the logical conclusion if the leaf originated from a much branched stem system; if the leaf is an organ distinct in nature from a stem, then the question of whether the primitive leaf is simple or compound is an open one and not predetermined by a theory. Let us examine the leaves of ferns from this point of view.

First of all, what are the facts regarding the occurrence of simple and compound leaves in the ferns? In almost every large family as well as in genera represented by a large number of species are ferns having leaves with all stages of division of the blade from simple and entire to highly divided. For instance, the genus *Cyathea* which is usually thought of as characterized by gigantic decompound leaves, really has species with all degrees of division from the undivided leaf as in *Cyathea sinuata* Hk., to simply pinnate as in *C. brunonis* Wall., to bipinnatifid in *C. alternans* (Wall.) Pr., to bipinnate-tripinnatifid in *C. latebrosa* (Wall.) Copel., to tripinnate in *C. tripinnata* Copel.

The same is true of the family Hymenophyllaceae in which leaf blades range from simple and entire to 4- or 5-pinnate. It is more of a surprise to those acquainted primarily with the ferns of the northern United States to find that the same range of blade division may be found in the genus *Adiantum*. Several species of the simple-leaved maiden hair fern exist, one of which, *Adiantum parishii* Hk., grows in Burma. There are many species with 1-pinnate leaves such as *A. philippense* L. and *A. caudatum* L.; with 2-pinnate leaves as in *A. capillus-veneris* L., and with 3-pinnate leaves as in *A. cuneatum* Langsd. & Fisch. Similar series occur in *Asplenium* and *Diplazium*.

In some families and genera the highly divided leaves are missing or rare, and simple or 1-pinnate forms predominate as in *Phymatodes*. Sometimes a whole genus is characterized by simple entire leaves as in *Pyrrhosia*, but even here one is

not surprised to find species with palmatifid or pinnatifid blades. Evidently in such cases the series has never developed beyond the second stage. In other families and genera the simple end of the series may be missing as in *Microlepia* in which all forms from the 1-pinnate to highly compound are known. The potentiality for the development of this pattern of variation of the leaf blade is certainly present in most of the large families. This is so general that if one of the forms is not known from one section of the world, it probably can be found in some other or in fossil form.

Can it be established which end of the series is the more primitive? Foster (1936) in working with angiospermic leaves has shown that the blade develops from two elongated lateral meristems along the sides of the costa. If this develops uniformly without break, the blade is simple; but if the lateral meristem soon becomes localized rather than continuous, then the blade developed will be divided or compound. In other words, to get more highly compound leaves a more extreme development of localized and isolated blade meristems is necessary. Such a distribution of meristems seems to represent a more complex system of primordia than a simple continuous one along a continuous costa. To some extent the degree of division may increase somewhat with increasing size of the leaf unless the veins are very close together as in *Thamnopteris*, *Microsorium*, *Phymatodes*, and *Platycerium*.

Fertile juvenile leaves produced on the not yet fully mature stems of many species which normally have compound leaves such as *Drynaria quercifolia* and *Arthromeric wallichiana* are often simple or have very few lobes or pinnae. Ching says that far too many ferns have been described for China because juvenile forms with simple leaves have often been described as new species. The fact that juvenile leaves of many compound-leaved species precede the compound during ontogeny is not evidence that the simple leaf is more primitive than the compound, yet this occurrence does give an illustration of what takes place when a stem which has produced simple leaves begins to produce more divided ones. With increase in age and possibly in the size of the leaf primordia, there is a localization of the meristematic tissue referred to above which results in compounding. No case is known to the writer where leaves produced by increasingly mature plants are less divided than the leaves produced earlier unless the complicating factor of reproduction begins to operate. If the highly divided blade be the primitive form as so widely accepted, then we will have to conclude that as a fern plant reaches maturity, its leaf-form reverts more and more to the primitive condition. That this could be almost universally so seems hard to credit.

If any portion of a blade be more highly divided than another, it is the basal part as illustrated by *Lindsaya orbiculata* (Lam.) Mett., in which several basal pinnae are again pinnate, and the upper pinnae are entire or only slightly incised. This is true for most ferns which have deltoid leaf blades. The lower pinnae are formed before the apical ones, originate from larger lateral pinnal meristems, and are less quickly determinate in their growth than the apical pinnae. In fact these lower pinnae tend to repeat the architecture of the apical portion of the main blade and to approach it in size. The more highly divided lower pinnae of many species is an indication of the tendency to a greater degree of division of the blade.

One of the common variations in leaves is the cresting or forking of the pinnae of such ferns as *Nephrolepis*, *Osmunda*, *Polystichum*, and *Pteris*. Bower (1923) says that such cresting is essentially reversion. Tryon (1938) considers the fluctuating types of cresting as reversionary, but the heritable kinds as advance. Conley (1944) has shown that in some of the crested varieties of *Nephrolepis exaltata* that a correlation exists between anatomical differences and chromosome number and that none of the forms studied seemed to represent the parent diploid complex. Such evidence seems to indicate that cresting in *Nephrolepis* is associated

with polyploidy, hybridization, or reduction of chromosome number below the normal diploid complement. If there is no evidence that cresting with the consequent greater division of the blade is an advanced character, at least there seems to be no ground for hasty conclusion that it is reversionary and that the divided condition of the blade is primitive.

All of the above lines of evidence seem to point to the correctness of the view that variation in the fern leaf progresses from simple to divided and compound.

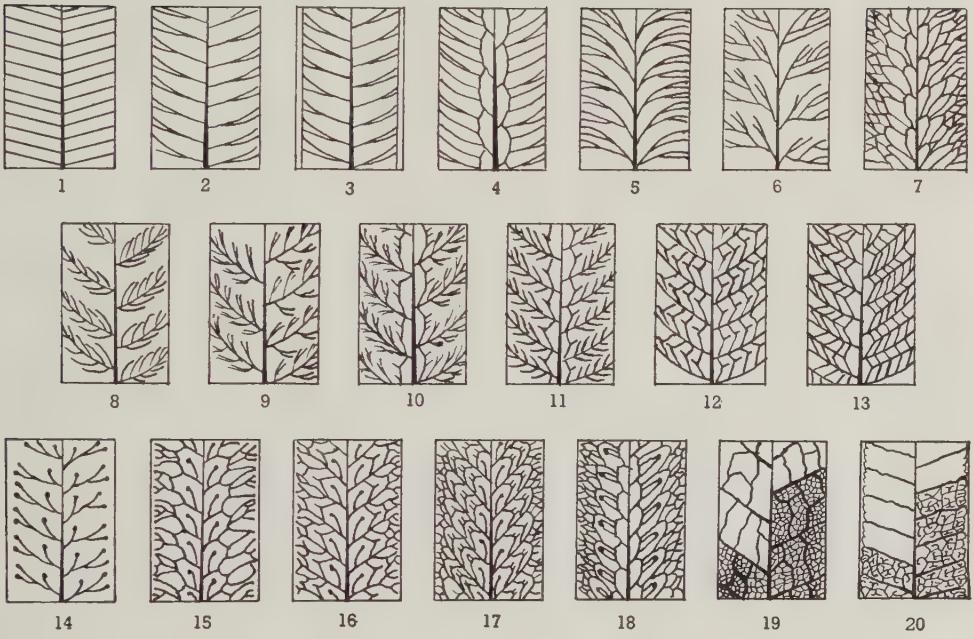
12. Venation. If Wardlaw's hypothesis (1944a) to account for the initial differentiation of vascular tissues in ferns should hold for the veins of the leaf, then different venation patterns would result from amazingly different patterns of growth in the leaf blade; for Wardlaw suggests that the initial differentiation of vascular tissue takes place immediately below or behind a meristematic center and "in the path of substances diffusing from it, one or more of these substances being casually involved in the process." If this is true, then the venation would be the blueprint of the pattern of growth of the leaf blade, particularly complicated in leaves with reticulate venation. Since no other more probable working hypothesis has been proposed to date, we shall examine the evidence from this point of view.

When the apical meristem of the leaf primordium divides by equal dichotomy, the main veins are dichotomously branched as in *Dipteris conjugata;* when the apical meristem divides unequally and one sidedly, catadromic helicoid main veins result as in *Matonia pectinata* and *Adiantum pedatum*, or anadromix helicoid main veins as in the fossil *Dictyophyllum exile*. If the apical meristem divides by unequal dichotomy, the subordinate shanks being alternately right and left, a zigzag or geniculate midrib or rachis develops which appears to be a continuation of the petiole. An extreme example is *Rumohra diffracta* (Bak.) Cl. Bower (1923) points out that when such a central axis of the blade is well developed, the primordia of the lower pinnae appear at a point below the apex of the leaf as lateral outgrowths upon it. Such branching of the axis is, in reality, monopodial. No clear line can be drawn between the monopodial and extreme cases of unequal dichotomy where alternate shanks develop into the subordinate branches. The architecture of the leaf may be determined, then, by the type of branching of the apical meristem, whether by equal or unequal dichotomy or by monopodial division.

The secondary veins in the pinnae or ultimate segments of the blade are exceedingly varied. Where the apical meristem of the leaflet primordium divides dichotomously from the beginning, a dichotomous pattern of veins is produced as in many species of *Lindsaya, Adiantum* and *Asplenium*.

Where the apical meristem of the leaflet maintains its dominance, a midrib is produced and lateral veins grow outward from along its sides in a pinnate pattern presumably developing immediately back of meristematic centers located on the margin of the leaflet primordium. When these centers are close together, simple, unbranched, costaeform veins result, Fig. 1. Where some of the meristematic centers divide equally, once-branched veins are formed as in some species of *Oleandra*. Fig. 2. These lateral veins may be free and end at or near the margin, or they may be united at their tips by a connecting marginal vein as in *Thamnopteris*, Fig. 3. Where the meristematic centers are further separated on the primordial blade margin, they tend to divide dichotomously more than once to form a fascicle as in *Osmunda javanica*, Fig. 4. Where the shanks of the dichotomy are unequal, a fascicle is formed intermediate between a sympodium and a monopodium as in *Asplenium adiantum-nigrum*, Fig. 5.

In some species the lowest veins of adjoining fascicles grow toward each other and unite, forming an arching vein more or less parallel with the costa, from which arch grow out either simple or once-branched veins as in *Brainea insignis*, Fig. 6. Or the branches of adjoining fascicles may unite to form uniform areoles without



TYPES OF VENATION

EXPLANATION OF FIGURES 1–20

NOTE: The names of the types of venation are those proposed by Georg Mettenius (1856).

Fig. 1. Costaeform venation.
Fig. 2. Taeniopteroid venation as in *Oleandra*.
Fig. 3. Venation as in *Thamnopteris*.
Fig. 4. Neuropteroid venation as in *Osmunda javanica*.
Fig. 5. Sphenopteroid venation as in *Asplenium adiantum-nigrum*.
Fig. 6. Venation as in *Brainea insignis*, approaching the Doodyoid type.
Fig. 7. Sagenioid venation of *Schizoloma ensifolia*.
Fig. 8. Pecopteroid venation as in *Matteuccia orientalis*.
Fig. 9. Pecopteroid venation as in *Cibotium barometz*.
Fig. 10. Pleocnemioid venation as in *Pteris biaurita*.
Fig. 11. Venation as in *Cyclosorus*.
Fig. 12. Goniopteroid venation as in *Abacopteris*.
Fig. 13. Goniopteroid venation as in *Goniopteris prolifera*.
Fig. 14. Eupteroid venation as in *Polypodium vulgare*.
Fig. 15. Marginarioid venation as in *Polypodium amoenum*.
Fig. 16. Goniophlebioid venation as in *Polypodium subauriculatum*.
Fig. 17. Cyrtophlebioid venation as in *Cyrtomium falcatum*.
Fig. 18. Phlebodioid venation as in *Polypoidum aureum*.
Fig. 19. Drynarioid venation as in *Drynaria quercifolia*.
Fig. 20. Anaxetioid venation as in *Lepisorus*, *Microsorium*, and *Phymatodes*.

free included veinlets as in *Schizaloma ensifolia*, Fig. 7. In many natural genera there are sections with free veins and others in which the venation is similar except that some or all the veins unite to form regular areoles without free included veinlets, as may be illustrated by the following genera or sections:

Veins free	*Veins anastomosing*
Lygodium	Lydodidictyon
Aneimia	Aneimidictyon
Davallia	Diellia
Pteridium	Lonchitis
Pteris	Histiopteris
Asplenium	Asplenidictyon
Diplazium	Allantodia

It is evident from such a list as this that free and reticulate venation are not two fundamentally different things, but rather that reticulate venation may develop from the open type wherever a diverging meristematic center on the margin of the blade primordium meets and merges with an adjacent center.

In simple leaves, leaflets, or ultimate segments of a compound blade the fascicles of veins which arise from the midrib may be pinnately branched, not forked as in some of the foregoing examples. These branches may themselves be simple and unforked as in *Matteuccia orientalis*, Fig. 8, or forked as in *Cibotium barometz*, Fig. 9. The lowest veins of adjacent fascicles may unite to form a costal arch with free excurrent veinlets as in *Pteris biaurita*, Fig. 10, and *Cyclosorus*, Fig. 11. Sometimes all of the lateral veins may unite angularly with excurrent veinlets which may or may not extend to the next higher pair of united veinlets as in *Abacopteris*, Fig. 12, and in *Goniopteris prolifera*, Fig. 13.

A fourth general pattern of venation is found in the Polypodiaceae. In the ultimate lobes or segments there may be veinlet fascicles in which the lowest branch on the side towards the apex of the segment is short and quickly determinate, not reaching the margin. The other branches of the same fascicle may be free and nearly reach the margin as in *Polypodium vulgare*, Fig. 14; or they may unite forming one row of areoles with free excurrent veinlets running to the margin, as in *Polypodium amoenum*, Fig. 15; or they may unite to form two or more rows of areoles with one excurrent veinlet in each areole as in *Polypodium subauriculatum*, Fig. 16; or with several excurrent veinlets in each areole as in *Cyrtomium falcatum*, Fig. 17. A variation of this pattern in which the two included veinlets meet and fuse, gives the venation of *Polypodium aureum*, Fig. 18. A second modification of the type of venation in Fig. 17 may have given the close reticulum without free included veinlets found in *Drynaria quercifolia*, Fig. 19. Still a third modification of the same venation, in which the free included veinlets are irregularly oriented, appears in *Lepisorus*, *Microsorium* and *Phymatodes*, Fig. 20.

To summarize, it may be said that several patterns of variation of the veins of fern leaves exist, and that in general in each series open venation represents a simpler growth pattern of the margin meristematic centers in the leaf primordia than does reticulate venation.

13. Fertile areas of the leaf. One of the first things that attracts attention in the study of fertile leaves of such genera as *Osmunda*, *Aneimia*, or *Polystichum* is that the area of the leaf which is fertile varies markedly in different ferns. In

EXPLANATION OF PLATE II

Fig. 21. Unilaterally dimorphic leaf of *Onoclea sensibilis*.
Fig. 22. Unilaterally dimorphic leaf of *Pteris cretica*.
Fig. 23. Hemidimorphic leaf of *Osmunda cinnamomea* forma *frondosa*.
Fig. 24. Series of leaves of *Onoclea sensibilis* from vegetative to reproductive.

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some cases the transition between fertile and sterile regions is gradual, in others abrupt. By a study of certain species in which the leaf is fertile only in part, we may reach conclusions very different from that reached by Bower (1923) when he states, "The lower parts of the leaf are more exposed, and this may explain the frequent absence of sporangia at the base. *Osmunda regalis* is an example of this."

Thus, *Osmunda regalis* may have only a few of its apical pinnae fertile, but in any large collection specimens may be found which show many more fertile upper pinnae, perhaps all on the upper half of the leaf. *Osmunda japonica* of Burma has a sporophyll of which all the pinnae are fertile from the apex to the base, though in other respects it is identical with *O. regalis*. Evidently we have here a physiological condition which in *O. regalis* does not become established until after the "foliar determination" (Foster, 1936) of the basal and first formed part of the leaf has become fixed in a prospective vegetative course of development. In *O. japonica* the condition changes from the vegetative to the reproductive state earlier in the ontogeny of the leaf, with the result that the entire blade is fertile. Similarly in *Polystichum acrostichoides* specimens may be found which vary from those having only a few apical pinnae fertile to those in which all but the lowest few are fertile. Here again there must be a variation in the time at which the change takes place from the vegetative to the reproductive condition. Where the change is early enough in the ontogeny, the whole blade may be fertile.

Osmunda cinnamomea which normally has the sporophyll completely fertile from base to tip, sometimes has leaves in which the apical half only is fertile. In literature this is called *Osmunda cinnamomea* forma *frondosa*, Fig. 23. Porter (1930) reported leaves with only one or two fertile pinnae at the top. Had the shift to the reproductive condition come any later in such leaves, there would have been no fertile pinnae at all. It may be inferred from such examples that physiological states are involved, that where a shift occurs from the vegetative to the reproductive state late in the ontogeny of the leaf, only the tip is fertile; but that with a progressively earlier change to the reproductive condition, more and more of the leaf becomes fertile until a completely fertile leaf is produced.

In species such as *Osmunda vachellii* Hk. only the basal pinnae are fertile; evidently here the change from vegetative to reproductive state, comes in early during the development of the leaf, but quickly shifts back again to the vegetative with the result that the later-formed parts of the blade are purely vegetative. In the very similar *O. javanica* Bl. the temporary shift from the vegetative to the reproductive condition comes slightly later, with the result that a few medial pinnae are fertile. The same timing exists in *O. claytoniana*, our common interrupted fern, in which from one to six medial pinnae may be fertile, depending on how long the reproductive condition remains. It is possible to conceive of a growth substance, a sporogen, as being involved in such shifts of the physiological condition.

A study of certain cases of unilateral dimorphism, in which one side of a leaf is fertile and the other sterile, may provide further evidence, for example, a specimen of *Onoclea sensibilis* from Ohio, Fig. 21, of *Pteris cretica* from the Himalayas, Fig. 22, and of *Dryopteris thelypteris* mentioned by Blake (1933). Evidently the physiological condition on one side of the leaf was continuously reproductive while, at the same time, that operating on the other side was continuously vegetative. In each of these species there are two leaf traces entering the petiole base. It would seem that the hypothetical hormone regulating spore production might be supplied through one trace to one side but not through the second trace to the other side: no cases of such unilateral fertility have been found by the writer in leaves having other than two leaf traces. Whatever it is that regulates spore production, it must be able to work in this unilateral manner at least when two leaf traces are present, as well as in the vertical zonal manner already referred to.

Although no general survey has ever been made as to the occurrence of different fertility patterns, the least frequent pattern is probably that in which only a few pinnae near the middle of the leaf are fertile; the next more frequent, that in which only the basal part of the blade is fertile. Probably the most common pattern is that in which the leaf is fertile to varying degrees from the tip downward, often resulting in a completely fertile leaf.

Knowing no more than we do about the real cause of the change from the vegetative to the reproductive state, it is difficult to establish one fertility pattern as more advanced than another. Until further facts become known, we shall work on the supposition that there is a progressively earlier shift from the vegetative to the reproductive condition of the leaf during the ontogeny of the plant, and that there is a progressively increasing duration of the reproductive state once it has been initiated.

14. Vegetative and reproductive leaf forms. Dimorphism of the vegetative and reproductive leaves, or parts of leaves, is rather commonly supposed to be more or less restricted among the eusporangiate forms to the Bortychiales, and to *Osmunda* and a few other genera such as *Matteuccia* and *Onoclea* among the leptosporangiate ferns. The idea of such a restricted occurrence of dimorphism arises, perhaps, from a study of the rather meager American fern flora in which there are comparatively few cases of dimorphism. Though general in the Ophioglossales, dimorphism is by no means limited to that order. In both the Marattiales and the Filicales examples of dimorphism are to be found in most of the families and in over 55 genera.

Dimorphism is neither limited to one phyletic line nor restricted to ferns of any one habit or habitat. Extreme forms of dimorphism are illustrated by such aquatic ferns as *Ceratopteris thalictroides*, by such swamp ferns as *Osmunda cinnamomena*, by such mesophytic ferns as *Bolbitis*, *Egenolfia*, and *Plagiogyria*, by such epiphytes as *Platycerium* and *Drymoglossum*, by such xerophytes as *Pteris cretica*, and by such climbing ferns as *Stenochlaena*. Evidently dimorphism has not arisen in response to any given set of environmental factors, and cannot be considered as "adaptive."

There are varying degrees of difference between the vegetative and fertile parts, from subdimorphism to extreme dimorphism. Where such differentiation appears in different parts of the same leaf, the term *hemidimorphism* is used instead of *dimorphism*. The modification involved in the differentiation of the sporophylls are many and varied, as may be seen from the following tabulation of differences:

1. Length of the petiole: the petioles of the sporophylls may be longer than those of the vegetative leaves as in *Hemionitis arifolia*, or shorter as in *Matteuccia struthiopteris*.

2. Expansion of the blade: The blade of the sporophyll may expand during ontogeny only slightly or none at all, as in *Egenolfia*. A similar contraction of the sporophyll is evident in the Cycadophyta.

3. Shape of the blade: the blades of the sporophylls may be of a different shape than those of vegetative leaves. For example, sporophyll blades of *Drymoglossum pilosiloides* and *Phymatodes rhyncophylla* (Hk.) Ching are linear and the vegetative blades round or oval.

4. Leaf margin: the margin of the sporophyll as of *Pteris cretica* may be entire, that of the vegetative leaf toothed.

5. Degree of dissection: the sporophyll may be much more deeply lobed or divided than the vegetative leaf as in *Doryopteris ludens*, or much less deeply lobed or divided as in *Riphidopteris peltata* (Sw.) Schott.

6. Synthesis of chlorophyll: the sporophylls may lack chlorophyll as in *Osmunda japonica*. A similar condition is found in *Equisetum arvense*, the most advanced of the horsetails.

7. Duration of the leaf: sporophylls may be very ephemeral as in *Osmunda cinnamomea*.

8. Season of production: in some ferns such as *Osmunda japonica*, the sporophylls appear before the vegetative leaves; in others such as *Ceratopteris*, *Onoclea*, and *Matteuccia* they appear much later.

Explanations of many different kinds have been offered to account for dimorphism. "Physiological advantage" has been invoked by Copeland (1907, 1929a); "use and disuse," by Clute (1908). When it is recognized, however, that dimorphic and monomorphic species grow side by side in the same habitat and survive equally well, such explanations become mere hypothetical modes of escape.

Some evidence from intermediate forms of normally dimorphic species such as *Osmunda cinnamomea* has been offered by Clute (1905) to show that injury to the rhizome may affect the degree of dimorphism of the leaves produced, but Breckenridge (1917) showed that such injury was not involved in the production of intermediate forms of the leaves of *Onoclea sensibilis*. Road tar was suggested as the cause of the production of the *frondosa* form of *Osmunda cinnamomena* (House, 1933), but leaves of this type have been found by the writer where no such material was present. Atkinson (1894) claimed that a modification of the nutritional balance of the plant through the removal of all vegetative leaves resulted in the production of leaves intermediate between the sterile and reproductive, but similar observations made by Breckenridge (1917) failed to confirm the earlier results. Atkinson (1911) also claimed that fire injury could be the cause of intermediate forms. Price (1912) and Weatherby (1937) considered that light intensity and moisture conditions affect the degree of blade expansion of sporophylls. However, none of the suggested environmental factors can explain the existence of dimorphism itself.

Unfortunately there is very little definite information about the growth and differentiation of the tissues of fern leaves; for this reason it is impossible at present to explain just what happens when the expansion of the fern leaf is inhibited at the time of spore production. The fact that dimorphism is normally associated with areas which are reproductive shows that both the change in the anatomy of the leaf and the production of sporangia are consequences of the same factor or complex of factors. It would seem that in some ferns the hormones that induce spore production modify the effects of growth substances probably associated with the lateral meristem which develops the blade. That this inhibiting action may be slight, medium, more marked, or extreme is beautifully illustrated by forms of *Onoclea sensibilis*, Fig. 24, in which a closely graded series of leaves may be found from the fully expanded and slightly lobed, wholly vegetative leaf, through forms increasingly smaller, more deeply lobed, and sometimes sparsely sporogenous, to the extremely reduced fertile blade with bead-like, fertile, inrolled lobes.

The production of sporophylls and vegetative leaves at different seasons may well be a photoperiodic phenomenon. Small plants of *Ceratopteris thalictroides* (L.) Brongn., placed by the author in the greenhouse at Ohio State University on July 7, 1945, under 14-hour summer day-length, began producing sporophylls by August 8, whereas it was not until September 1 that plants kept in light of 8-10-hour duration produced the first sporophyll (and that only after the plants had received, by accident, full length summer daylight over a weekend). On six plants kept under continuous light only one sporophyll was produced by September 25th; the vegetative growth was luxuriant. It would seem possible that the photoperiod regulates the formation of the sporogen. Further experiments, more critically controlled, should be conducted with *Ceratopteris*.

The phylogenetic significance of dimorphism of vegetative leaf and sporophyll is evident from a survey of the vascular plants as a whole. Sporophylls, including stamens and carpels, being organs homologous with vegetative leaves, (Bower, 1923) are considered more advanced the more they differ from vegetative leaves. There is a progression from the generalized processes of a double-duty, monomorphic

leaf to the more specialized processes of dimorphic leaves. Monomorphic leaves are held, therefore, to be more primitive than hemidimorphic or dimorphic leaves. A genus in which dimorphism is characteristic is to be considered more advanced than a genus with largely monomorphic leaves, other characters being similar. There seems to be no factual basis for distinguishing primitive and advanced types of dimorphism as Eames (1936) does except as a consequence of the cladode hypothesis of leaf origin which is here considered as untenable.

15. Dimorphism of vegetative leaves. Some ferns have in addition to sporophylls two kinds of vegetative leaves. For instance, *Matteuccia struthiopteris* has bipinnatifid vegetative leaves on its upright stems, and in addition has large scale-leaves on its prostrate stems. The high-climbing ferns *Lomagramma* and *Teratophyllum* (Holttum, 1937a, 1937b) have acrophylls which are the leaves formed at high levels in the forest, and bathyphylls which are formed at the ground level. These upper and lower vegetative leaves differ in shape and degree of division of their blades. The epiphytic fern, *Drynaria*, has deeply-pinnatifid and long-petioled ordinary vegetative leaves, and sessile, less deeply-pinnatifid sterile leaves in the axils of which humus often collects. The primordial patterns of species having several kinds of leaves are considered to be more complex, and therefore more advanced, than those of a species having only one kind of leaf.

16. Position of the sori. Basing their speculation on the cladode hypothesis of the leaf and the psilophytan origin of the ferns, Bower (1923) and those following him (Eames, 1936, Campbell, 1940, etc.) concluded that the position of the sori at the margins must be more primitive than that on the abaxial surface of the leaf. These authors arrived at this conclusion by reasoning that since the sporangia of the postulated primitive types were apical on the branches, and since leaves are considered to be simply branches of a stem which had become united by webbing, then the marginal position of sori on a leaf blade would correspond with the apical position on unwebbed branches. These are quite logical deductions from highly speculative premises. Advance, from this point of view, would consist in any shift of the sori from their marginal position to the abaxial surface of the blade, a movement called by Bower (1923) "the phylogenetic slide." So fundamental does Bower think the soral position to be that he uses it as the primary character on which to base his three phyletic lines of leptosporangiate ferns: the Marginales, the Superficiales, and the non-soral Osmunda-Gymnogrammeoid line.

On the other hand, if the theory be accepted that in the phylogenetic development of the sporophyte of the Metathallophyta there has been a progressive movement of spore production from the central axis to the periphery of the sporophyte, then the logical conclusion would be that marginal sori are more advanced than those on the abaxial surface because they are at the determinate limit of movement away from the axis of the sporophyte.

Copeland (1907) has proposed that the advanced position of the sorus is that reached by the adaptation of the reproductive structures to their habitats: "The principles underlying the adaptations of the reproductive structures of ferns are very simple. . . . The mature spores must dry thoroughly enough to be easily and well scattered, and yet the drying of the spore must not involve too great a dessication of the frond." Since the marginal or apical position of the sori permits spore distribution without undue drying of the blade, the marginal position would thus be one of the most advanced. This is pure and quite unnecessary teleological theorizing.

Deductions such as those drawn from the preceding three theories may be logical but not necessarily fit the facts. Let us therefore examine the soral positions and see whether the question of what is primitive and what is advanced may be settled aside from an appeal to these philosophical theories. Sori occur at the

following places on fern leaves: first, lateral on the veins on the abaxial surface of the leaf blade, or very rarely on the adaxial side as in *Polystichum anomalum* J. Sm.; second, lateral on the veins and on the epidermal tissue between the veins, a condition usually called acrostichoid; third, apical on the veins. In some cases the veins end at the leaf margin so that apical sori and marginal sori become the same; in other cases, Figs. 14–18, 20, some veins end far short of the margin; sori terminating such veins are superficial on the abaxial surface.

From dry herbarium specimens of acrostichoid species with much contracted sporophylls, it is difficult in most cases to ascertain whether the sporangia are really scattered over the surface or are borne on linear or punctiform receptacles which are very close together as a result of lack of expansion of the blade. Fresh material and occasional intermediate forms of sporophylls, which are partially expanded, provide enough evidence to permit a decision.

A distinction between sori which are apical on veins and those which are lateral on them is far more fundamental than a distinction between sori which are marginal and those which are "superficial" on the abaxial surface, inasmuch as sori apical on veins may be either marginal or surficial. According to Bower's scheme, *Nephrolepis* belongs to the Marginales group, yet in most of the species the sori are not marginal but definitely intramarginal or medial. Bower would explain this situation by saying that a phylogenetic slide of the sorus from the margin to the abaxial surface has taken place in *Nephrolepis* so that the sori are no longer truly marginal. Certainly such a system is taxonomically very unusable because many species with "superficial" sori are placed in the Marginales and many species with marginal sori are placed in the Superficiales.

Whether the sori of *Nephrolepis* are medial, intramarginal, or marginal, in all cases they are apical on veins. The same may be said of the rest of the Davalliaceae which vary as much in the relation of their sori to the margin as does *Nephrolepis*. The true relationship of all these species is shown much more clearly by the common apical position of their sori on the veins than by the relation of these sori to the leaf margin.

Let us further test the value of the marginal-superficial category of Bower and the apical-lateral interpretation presented here. *Oleandra* is a very natural genus whose relationship has always been doubtful. Bower, however, included the genus with his Davallioid ferns, a group forming a part of his Marginales line. The sori of *Oleandra* are neither marginal, intramarginal, or even medial; in all known species without exception the sori are costal, that is, located close to the midrib. Here the phylogenetic slide must have been complete! How very unnatural, then, to place *Oleandra* in the Marginales. On turning to a consideration of the position of the sori on the veins, we find that the sori of none of the oleandras are terminal on veins, in contrast to the universally apical sori of the Davalliaceae; rather they are all lateral on the veins and close to the midrib. It seems to be clear than *Oleandra* should neither be included with the Davallioid ferns nor placed in the Marginales, but rather that their affinity is with the Thelypteroid-Asplenioid ferns.

Although in a great majority of the ferns the sori are clearly either lateral or apical on the veins, there are some soral conditions which are very difficult to interpret. The distinction between the apical and lateral positions on veins disappears in two cases: first, if sori apical on the veins spread inward along the veins, and second, if sori lateral on the veins extend outward to the apex. Tryon (1942) has suggested the possible phyletic movement of the receptacle in the tribe Cheilantheae: "The receptacle can be thought of as having moved toward the vein-ends which were then correspondingly expanded, and finally to have spread laterally, the adjacent vein-ends connecting." He begins his series in this tribe with *Eunotholaena* in which the sporangia are on the terminal one-half or one-fourth

of the little-modified veins, and carries it through *Cheilanthes*, whose sporangia are on clavate or flabellate vein-ends, to *Doryopteris* in which the sporangia are borne on a continuous commissure connecting the vein-ends. Tryon interprets the series as a movement of the sori outward from the terminal portion of the veins to the enlarged and expanded vein-ends.

Chowdhury (1932), from the study of subdimorphic pinnae of *Osmunda claytoniana* and of extinct osmundaceous ferns, concluded that the primitive position of the sori of these ferns is superficial on the abaxial surface of the blade. But with the total failure of the fertile pinnae to expand, the sporangia appear to be marginal although actually they can be neither marginal nor superficial since there is no blade expansion. Chowdhury's conclusion that for the Osmundaceae the abaxial superficial position of the sori is primitive is directly opposite to the conclusion of Bower (1926) that the originally marginal sporangia passed to a superficial position on the abaxial surface. The writer agrees with Chowdhury and Harris (1931) that in this family the unspecialized members show the sori to be lateral on the veins and not apical or marginal.

Is there any direct evidence to indicate whether the apparent spread of the sori has been toward or away from the apices of the veins? So far as the writer knows there is no direct evidence which tips the balance of decision one way or the other. Until something definite is known as to the nature of the control involved in sorus initiation, no satisfactory solution is likely to be forthcoming. Certainly it is unwise to prejudice the whole case by accepting the uncertain cladode theory of the leaf and the psilophytan ancestry of the ferns. Assuredly no appeal to "physiological advantage" can settle the question, as ferns with sori in all positions live side by side; one position would seem to be as good as another. Should the idea be true that there has been a movement of spore production from the center of the axis to the periphery of the sporophyte in the Metathallophyta, we could conclude that those sori which are apical on veins are advanced because they have reached the determinate limit of the movement toward the periphery of the plant body.

To summarize, then, ferns may be divided into two groups, the first characterized by sori borne laterally on the veins, their position ranging from very close to the midrib to the apex of the veins themselves. If the venation is reticulate, the sori may be at the point of union of veins. Probably derived from this group are the species with acrostichoid sori. The second group is characterized by sori normally located at the apices of veins which may or may not be expanded at the tip or be united by a vascular commissure. Certain ferns of this group which belong to the Polypodiaceae have veins which do not reach the leaf margin, Figs. 14–18, 20. The group also includes such families as the Dennstaedtiaceae, Lindsayaceae, Davalliaceae, Hypolepidaceae, Pteridaceae, Sinopteridaceae, and Adiantaceae in which all the veins reach the margin or equally near it.

17. Shape of the sorus. The sporangia of ferns are grouped in clusters called sori on circular, linear, or large and unrestricted receptacles. These receptacles are usually lateral or apical on veins, but in certain genera the receptacle may cover both veins and the epidermal tissue between them.

When the receptacle is small and circular, the sorus is punctiform. Should two or more receptacles occur so close together that their sporangia intermingle and appear to form one sorus, the resulting coenosorus is somewhat elongated as in *Bolbitis deltigera* (Wall.) C. Chr., *Drymoglossum*, and *Colysis*. Should the receptacle extend along a free vein, the sorus becomes linear as in *Asplenium* and *Diplazium*. If the receptacle extends along anastomosing veins, a reticulate sporangial pattern results as in *Hemionitis* and *Antrophyum*. If the receptacle extends along a vascular commissure connecting vein-ends, a continuous marginal sorus is formed. If the receptacle spreads from the veins to the adjacent epidermal

tissue as in *Acrostichum* and *Platycerium*, an acrostichoid sporangial pattern results.

Among the leptosporangiate ferns small receptacles on the veins may be considered primitive, and any fusion or elongation of receptacles, a derived condition. It is not to be inferred, however, from what has been said that soral shapes within genera are widely variable unless the occurrence of coenosori is sporadic or intermittent.

18. The indusium. Indusia are of regular occurrence in such genera as *Asplenium* and *Oleandra;* in others indusia may be of specific rather than generic occurrence as in *Cyathea* and *Thelypteris*. No indusia at all occur in the ferns included in the Polypodioideae by Christensen (1938); in nearly all of these ferns paraphyses are intermixed with the sporangia. Still another group of ferns including the Pteridaceae, Sinopteridaceae, Adiantaceae, and Ceratopteridaceae has modified and reflexed leaf-margins called false indusia. But no matter what these indusial scales, hairs, or flaps may be called, they are all fundamentally the same in that they are sterile growths occurring in proximity to sporiferous areas. Such elaboration of tissue is common in the higher plants—sepals, petals, corona, etc., of flowers, and the elaborate vegetative growth associated with the inflorescence of the Araceae. Although indusia may "protect" young sporangia, they should not be thought of as having arisen in order to carry out that function, but rather as vegetative out-growths associated with the development of reproductive structures.

In the Hymenophyllaceae and the Davalliaceae the indusium arises below the receptacle which terminates a vein, and varies from scale-like with basal attachment, to half-cup-shaped or tubular with basal and lateral attachment. In punctiform sori which are lateral on veins, the indusia may be inferior and calyx-like as in *Cyathea*, lateral and scale-like as in *Cystopteris*, lateral and reniform as in *Dryopteris*, or superior and peltate as in *Polystichum*. In other sori which are lateral on veins but with more or less elongated receptacles, the indusia may be elongate-reniform as in *Mesochlaena*, elongate and mostly unilateral but often hooked over the vein as in *Athyrium*, or completely unilateral as in *Asplenium*.

Infolded leaf-margins occur irrespective of whether the sori are indusiate or not: both infolded margins and indusia may be present as in *Onoclea* and *Marsilea;* infolded margins but no indusia occur in *Pteris*, *Onychium* and *Ceratopteris*.

The presence of indusia in contrast to paraphyses indicates neither an advanced nor a primitive condition, but simply a different expression of vegetative growth which occurs in the neighborhood of reproductive centers. The elaboration is localized in the one case, and is scattered throughout the receptacle in the other.

19. The order of sporangial development within the sorus. Bower (1923) recognizes in his main phyletic lines of the ferns three levels or conditions based on the order of development of the sporangia in the sorus: the Simplices, the Gradatae, and the Mixtae. He believes that these states of the sori "may severally have been achieved in accordance with biological advantage" along three distinct evolutionary lines. The Simplices include those ferns in which the sporangia develop simultaneously in any one sorus. The Gradatae are those ferns, in any one sorus of which the sporangia develop in basipetal or acropetal succession. The Mixtae are those in which the sporangia originate in irregular order.

Is this order of sporangial development of any phylogenetic value? The simultaneous development of sporangia occurs in the eusporangiate ferns and in such leptosporangiates as the Osmundaceae, Gleicheniaceae, Schizaeaceae, and Matoniaceae. These ferns are also characterized by their circular or elongated, unraised receptacles which bear from one to a few large sporangia. Of course where the sorus has but one sporangium as in *Lygodium* the order of development has no meaning. This simultaneous development of sporangia within each sorus

would seem to be a characteristic of those families which have a longer geologic history than the families in which the sporangia develop in succession. As a taxonomic character, therefore, soral development should take precedence over soral position which Bower uses to establish his three phyletic lines (Smith, 1938). In cases where simultaneous development is present in higher families, as in two genera of the Hymenophyllaceae, it is not associated with the same supplementary characters as those indicated for the more primitive families.

Bower's Gradatae and Mixtae really constitute but one group in which sporangial initiation and development is not simultaneous but rather successive. Species with a regular sequence of sporangial development are placed in the Gradatae; those in which "the sporangia of different ages are aggregated together without any definite sequence" are placed in the Mixtae. The essential similarity of the two groups is indicated by the fact that both regular and irregular sequences of development may be present in the same genus, as in *Dennstaedtia* or *Hypolepis*, and by the fact that in some ferns such as *Dennstaedtia rubiginosa*, *Cyrtomium* spp., and some of the Pteridaceae an initial regular sequence of development is followed by the interpolation of young sporangia in an unrecognized order.

The point to be emphasized is that receptacles of gradate sori are normally somewhat elongated-columnar as in *Trichomanes* and *Matteuccia*, peltate as in *Cyathea*, or dome-shaped as in some species of *Hymenophyllum* The acropetal or basipetal sequence in sporangial development seems to be expressed where some such elongation of the receptacle is present.

The receptacles of the "mixed" sori are normally flat or only slightly raised. No one physiological gradient from apex to base of the receptacle, or vice versa, seems to exist: the writer believes that a careful study of the development of these mixed sori should be made to determine if the pattern of succession of the sporangia is not unapparent rather than lacking as is true in a condensed cymose inflorescence.

For the present, therefore, it seems wise to give up the idea of three fundamentally different "soral states" suggested by Bower, and to think, rather, of two sections of the homosporous leptosporangiate ferns: the first with sori in which there is a simultaneous development of the sporangia, and the second with sori in which there is usually a successive development of sporangia. The first group is further characterized by sporangia which are large and relatively few per sorus, most of which also open by longitudinal dehiscence. The second group is usually characterized by sporangia which are relatively smaller and more numerous, which usually dehisce transversely.

Although it is unlikely that the group of ferns characterized by the simultaneous development of sporangia in the sorus has directly given rise to the group characterized by successive sporangial development, it seems tenable that the latter are more advanced than the former.

20. The sporangium. It should be made clear at the outset that the beautifully perfect mechanism of the polypodioid type of sporangium has not arisen due to any continued experimentation on the part of the plant and subsequent selection of the most biologically advantageous forms. The oblique annulus of the Gradatae does not become vertical because "the oblique position would be mechanically inconvenient when the receptacle is flat" as suggested by Bower (1935), but rather heritable protoplasmic factors are responsible for the variation and modification of the fern annulus.

In that group of leptosporangiate ferns with simultaneous sporangial development, the annulus consists of a cluster of thick-walled cells located near the apex of the sporangium, as in the Osmundaceae, or of an apical ring with a 1-celled apical plate as in the Schizaeaceae, of a horizontal ring with a large apical plate as in the Gleicheniaceae, or of an irregular and variable incomplete ring as in the

Matoniaceae. Dehiscence is median longitudinal except in *Platyzoma* and *Matonia*. The sporangia are sessile or short-stalked, the stalks being more than three cells thick. The spore-output per sporangium (Bower, 1923) varies from 1024 to 16: in the Osmundaceae from 512–256, in the Schizaeaceae from 256–128, in the Gleicheniaceae from 1024–512 in *Gleichenia flabellata*, to 256 or less in *G. linearis*. In *Platyzoma* the spore-count varies from 32–16, but there is considerable doubt whether this genus really belongs in the Gleicheniaceae.

In that group of the leptosporangiate ferns with successive sporangial development, the annulus consists of a more or less complete ring which varies in orientation from oblique to vertical. This ring may be complete with either some or all of its cells thickened, or it may be incomplete and interrupted by the stalk of the sporangium. The thin-walled part of the ring, often forming the stomium, may be little modified or may be clearly specialized as lip-cells. Dehiscence is lateral and takes place in this thin-walled area, except in *Loxsoma*. The sporangial stalk varies from short to long, and is 4–3–1–cells thick. The spore-output per sporangium varies from 420 to 1: in the Hymenophyllaceae from 420–32, in the Cheiropleuriaceae 128, in the Cyathaeceae from 64–8, in most of the "Polypodiaceae" about 64, in the Sinopteridaceae from 64–12, in the Ceratopteridaceae from 32–16, and in the Marsilaeceae from 64 microspores to 1 megaspore.

In the past, sporangial characters have been largely used to segregate families. Most of the ferns that have a more or less complete vertical annulus have been put into the "Polypodiaceae." Actually there is a very marked variety in sporangial structure. For instance, the annulus is oblique in *Odontosoria retusa* (Cav.) J. Sm., complete and slightly oblique in *Polystichum deltodon* (Bak.) Diels and in *Neocheiropteris waltoni* Ching, complete except for the interruption by the stalk in *Cheiropleuria bicuspis* (Bl.) Presl, and very broad and exceedingly variable in *Ceratopteris*. In recent years the "Polypodiaceae" have been subdivided into many families, sometimes on the basis of sporangial characters but more often on other bases.

21. The time of sexual dimorphism. The time of appearance of sexual diversity in the life-cycle of plants varies at different levels of differentiation in the plant kingdom (Schaffner, 1923). At the most primitive level the appearance of sex differences takes place in the gametes themselves; their gametangia appear to be identical, as in the alga *Ulothrix*. The second level is that in which sex differences appear in the gametangia located on a common hermaphroditic prothallus, as in most homosporous ferns. The third level is that in which there are distinct male and female gametophytes as in the unisexual prothalli of *Onoclea* and *Matteuccia* (Mottier, 1910). A fourth level is that in which sex differentiation occurs at the initiation of the sporangia in the sorus. This results in the formation of micro- and megasporangia, and micro- and megaspores as in *Marsilea*. In the fifth level the differentiation occurs still earlier, at the initiation of the sorus, with the result that each sorus contains microspores or megaspores but not both. This occurs in *Salvinia* where the two kinds of sori are similar in appearance, and in *Azolla* where the sori are dissimilar. If sexual dimorphism began any earlier in the life-cycle, microsporophylls and megasporophylls would be formed, but this level has not been reached by any of the known ferns.

The preceding twenty-one patterns of variation occurring in the ferns provide a basis on which the ferns of Burma will be classified. It should be recognized, of course, that some of these patterns will be valuable primarily in the arrangement of species in their genera; this will be true especially of patterns of vegetative structures. Others, particularly those having to do with reproductive structures and the life-cycle, will be of use in working out the relationships of larger groups.

From such a review of the variations occurring in the leptosporangiate ferns certain deductions of phylogenetic interest may be drawn. (Cf. Schaffner, 1936.)

1. Phylogenetic development in general is not teleological and does not advance because of some assumed utility of organs or mechanisms.

2. Lamarkian and Darwinian evolutionary hypotheses receive no support from the detailed study of ferns.

3. There is no general correspondence between the taxonomic system and phylogenetic progress on the one hand, and environments on the other.

4. Phylogenetic development is postulated as the result of an intrinsic process which is dependent upon the fundamental organization of the protoplasm—a sort of "internal predestination."

5. Any one character may become more specialized while other important characters remain unchanged.

V. The Orders and Families of Ferns

Taxonomists who have contributed greatly in recent years to the understanding of the relationships of ferns include W. R. Maxon, E. B. Copeland, Carl Christensen, and R. C. Ching. Attention is particularly directed to Copeland's treatise, *The Oriental Genera of Polypodiaceae* (1929), to Christensen's most valuable revision of the Filicinae in Verdoorn's *Manual of Pteriodology* (1938), and to Ching's publication, *On Natural Classification of the Family "Polypodiaceae"* (1940b).

In the present study the fern families are placed in five orders, the Ophioglossales, Marattiales, Filicales, Marsileales, and Salviniales, as shown in Chart IV on page 105. In the past the family Marsileaceae has either been included with the Salviniaceae and Azollaceae in a separate order, the Hydropteridales, or has been included in the Filicales. Campbell (1904), Bower (1926), and Christensen (1938) have considered that the Marsileaceae are descended from Schizaeaceous stock. Eames (1936) agreed in general with this view but suggested that the family may have been derived from Gleicheniaceous ancestors. Smith (1938) thought that the Marsileaceae could not have been derived from the Schizaeaceae, and that their origin should be sought among the Hymenophyllaceae or the Cyatheaceae. To connect the Marsileaceae with any homosporous fern family is to assume a degree of change in heritable characters quite beyond that which a study of genetics would lead us to expect. It is wisest to place the Marsileaceae in a separate order, making no guesses at present as to the definite origin of this family.

The order Filicales, as here delimited, includes only the homosporous leptosporangiate ferns. Linnaeus (1753) classified the 190 known homosporous species of ferns under ten genera—*Osmunda*, *Onoclea*, *Acrostichum*, *Hemionitis*, *Polypodium*, *Asplenium*, *Pteris*, *Blechnum*, *Lonchitis*, and *Trichomanes*. As more and more ferns became known, most of these original genera became the bases of families. Presl, a century after Linnaeus (1850), classified the then known homosporous leptosporangiate ferns under 149 genera and 17 tribes or families. Although 5663 ferns belonging to the Filicales were known by 1906, Christensen classified them under only 136 genera and 8 families. We see here, linked with a three-fold increase in the number of species known, a reduction of over 50% in the number of families recognized. By 1938 Christensen recognized 9000 species and 200 genera belonging to the Filicales which he classified under 11 families, one of which, the "Polypodiaceae," he subdivided into 15 subfamilies; these, he suggested, might better be dealt with as families. Ching (1940), following this suggestion, divided the "Polypodiaceae" into 32 sections, to each of which he gave a family status. This is a large increase in the number of fern families, but it is in harmony with the present trend in splitting large and unwieldy taxonomic groups into smaller ones; for example, Copeland (1938) divided the species of the family Hymenophyllaceae into 33 genera in place of the two usually recognized.

Some of the families proposed by Ching will likely stand as natural groups, but not all of them. For instance, the Sphaerostephanaceae which Ching based on *Sphaerostephanos* J. Sm. (or *Mesochlaena* R. Br.) cannot stand. Smith, himself, (1841), repudiated his genus as having been founded on a misconception of the nature of the receptacle. Ching's "Sphaerostephanaceae" is based on the same misconception and must therefore be repudiated. Copeland (1941c) pointed out several other families which he considered to be unnatural, but for the present the writer is accepting 31 of the families which Ching has revived or proposed anew.

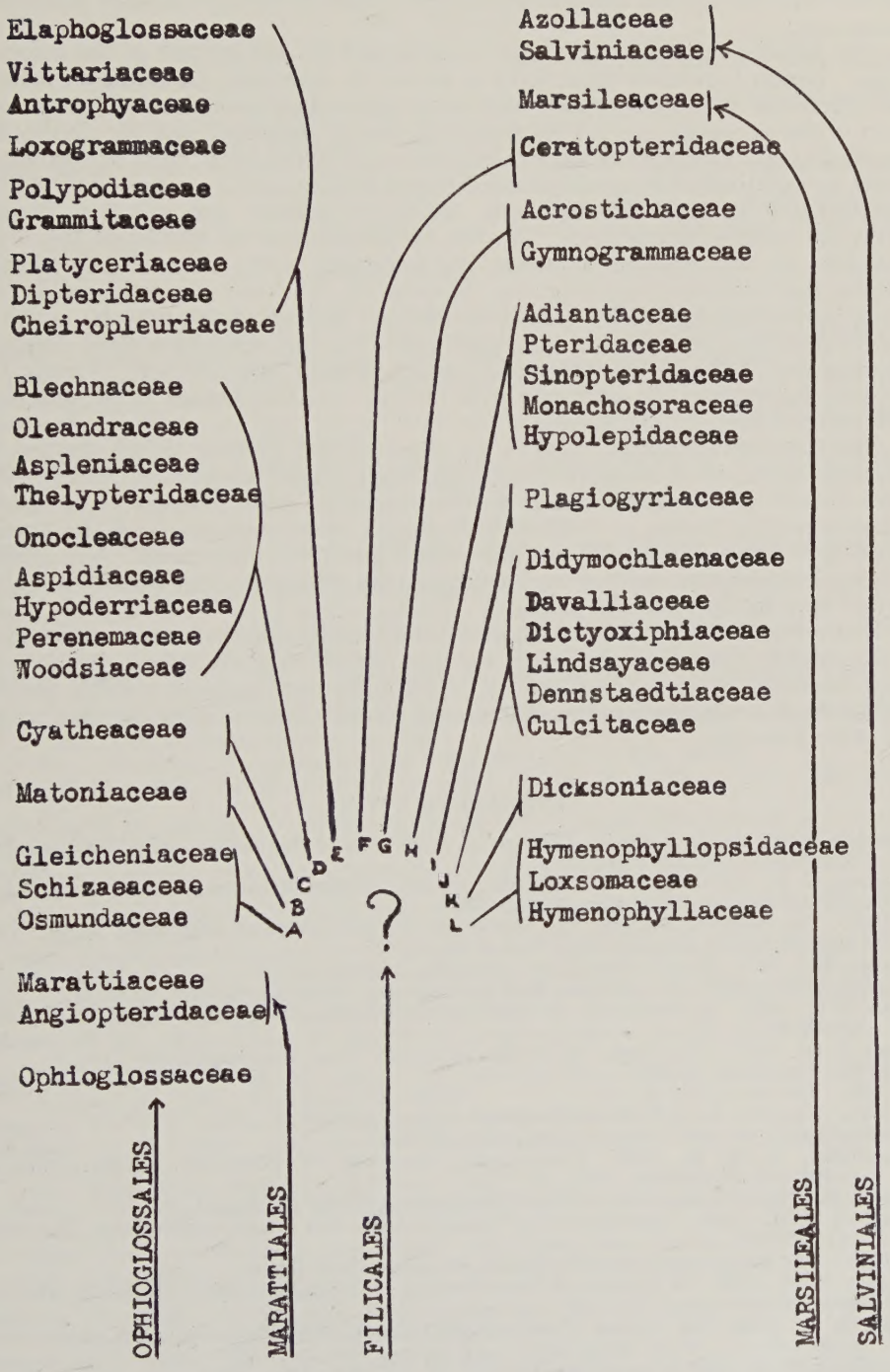
Bower, and following him Eames, Smith, and Campbell, have considered the "Polypodiaceae" to be polyphyletic. The Davallioid and Pteroid sections of the family they considered to have evolved from the Dicksoniaceae, and this family in turn from the Schizaeaceae. The Gymnogrammeoid ferns they believed to have originated from the Plagiogyriaceae, and this family from the Osmundaceae. The Asplenioid, Dryopteroid, Woodsioid, Onocleoid, and Blechnoid sections of the Polypodiaceae they considered to have originated from the Cyatheaceae, and this family from the Gleicheniaceae. The Dipteroid section they supposed to have originated from the Gleicheniaceae through the Dipteridaceae.

To some extent Ching, too, has been influenced by this polyphyletic concept. He arranges the 32 families segregated from the "Polypodiaceae" in six phyletic series as follows: first, a Lindsayoid-Devallioid series originating from Dicksonioid stock; second, a Pteroid-Gymnogrammeoid series originating from a similar ancestral stock; third, a Thelypteroid-Asplenioid series, with the Blechnoid ferns as an offshoot, originating from some extinct and unknown stock; fourth, a Cyatheoid-Aspidioid series originating from Cyatheoid stock; fifth, a Dipteroid-Polypodioid series, with the Elaphoglossaceae as an offshoot, originating from Dipteroid stock; and sixth, an isolated family, Didymochlaenaceae, originating from unknown stock.

The weak point of these theories which postulate the polyphyletic origin of the "Polypodiaceae" is the large amount of parallel development which they have to assume. How does it happen that all phyletic lines develop the same type of sporangium? As pointed out by C. A. Weatherby, we have been accustomed to think of evolution as largely a process of diversification; why, then, have these ferns produced a series of end members more alike than their ancestors were, and yet are to be kept wide apart because their ancestors are considered to have been different?

Actually there is little evidence to indicate that Bower's "Simplices"—the Schizaeaceae, Osmundaceae, and Gleicheniaceae—are really parent stocks which have given rise to three separate phyletic lines of ferns, of which each in turn gave rise to certain sections of the "Polypodiaceae."

In Chart IV the writer has arranged the families of the Filicales in generally related groups, without implying anything as to their origin. The ferns in Groups A–E are characterized by sporangia located in sori which are lateral on the veins on the abaxial side of the leaf. Group A includes ferns which are further characterized by exindusiate sori in which the sporangia develop simultaneously and dehisce longitudinally. Group B is further characterized by sori with superior peltate indusia, and by sporangia which develop simultaneously and dehisce laterally. Group C includes tree ferns with either exindusiate or indusiate sori. If present, the indusium is inferior and cup-like. The sporangia develop simultaneously in species having flat receptacles, and successively in species with elongated receptacles; the annulus is oblique and the dehiscence lateral. Group D includes those non-tree fern families, which normally have indusiate sori in which the sporangia develop successively. The sporangia have a more or less complete vertical annulus and dehisce laterally. Group E includes those non-tree fern


Elaphoglossaceae
Vittariaceae
Antrophyaceae
Loxogrammaceae
Polypodiaceae
Grammitaceae
Platyceriaceae
Dipteridaceae
Cheiropleuriaceae
Blechnaceae
Oleandraceae
Aspleniaceae
Thelypteridaceae
Onocleaceae
Aspidiaceae
Hypoderriaceae
Perenemaceae
Woodsiaceae
Cyatheaceae
Matoniaceae
Gleicheniaceae
Schizaeaceae
Osmundaceae
Marattiaceae
Angiopteridaceae
Ophioglossaceae
Azollaceae
Salviniaceae
Marsileaceae
Ceratopteridaceae
Acrostichaceae
Gymnogrammaceae
Adiantaceae
Pteridaceae
Sinopteridaceae
Monachosoraceae
Hypolepidaceae
Plagiogyriaceae
Didymochlaenaceae
Davalliaceae
Dictyoxiphiaceae
Lindsayaceae
Dennstaedtiaceae
Culcitaceae
Dicksoniaceae
Hymenophyllopsidaceae
Loxsomaceae
Hymenophyllaceae
A
B
C
D
E
F
G
H
I
J
K
L
?
OPHIOGLOSSALES
MARATTIALES
FILICALES
MARSIEALES
SALVINIALES

families which normally have exindusiate, paraphysate sori in which the sporangia develop successively and have a more or less complete vertical annulus and lateral dehiscence.

The families in Groups H–L are characterized by sori located at the apices of veins. Group L includes those ferns in which the sporangia are borne on more or less cylindrical receptacles usually with basal intercallary meristems. The development of the sporangia on the receptacle is usually basipetal, and the dehiscence, usually lateral. Group K includes those tree ferns having thick, erect or decumbent stems, sori with inferior cup-shaped or 2-lipped indusia, and sporangia with oblique annulus and basipetal development. Group J includes non-tree fern families which are usually characterized by sori each subtended on the basal side by a scale-like or half-cup-like indusium, by sporangia with more or less vertical annulus and successive development. Groups H and I are characterized by sori which are not subtended by indusia as above. The sporangia may be apical or may extend from the apices of the veins back along the veins for a short distance. The margins of the fertile leaves are usually reflexed over the sori. Group I is further characterized by sporangia with oblique annulus; Group H by sporangia with more or less vertical annulus.

The families in Groups F and G are characterized by lack of indusia, and by sporangia scattered on elongate receptacles which follow the veins and which sometimes extend to the epidermal tissue between the veins. Group G is further characterized by having no reflexed leaf margin, and by sporangia of the normal polypodioid type. Group F, on the other hand, is characterized by reflexed colorless leaf margins, and by very large sporangia with broad and variable annulus, located very far apart on the veins.

It is not to be inferred from Chart IV that the families in each group evolved in the order in which they are listed, nor that families originated from the immediately preceding ones on the chart. The grouping merely shows possible general relationships among the families of ferns and possible lines of diversification within the order Filicales.

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Reptiles of the Pacific World

This book is one of a series of seven books on the Pacific World, published under the auspices of the American Committee for International Wild Life Protection. Though it covers a wide field, it is a very readable and useful book.

There are separate chapters on the various groups of reptiles occurring in the Pacific area, chapters on poisonous snakes and the treatment of snake bite, a chapter on Pacific amphibians, and two chapters on collecting, preserving, and shipping specimens. At the end of the book is a chart showing the distribution in the Pacific of the various families of reptiles and amphibians, and a brief bibliography. The book contains numerous keys, and there are 70 line drawings illustrating the characters used in the keys. A great deal of space is devoted to accounts of the habits of the groups treated.

Except in a few groups, no attempt is made to present a complete taxonomic account of the Pacific forms. However, the reader will be able to identify a Pacific reptile or amphibian down to family, and often farther. The distribution chart will enable one to quickly determine what forms to expect in any island group, though it omits a few cases of introduced species. To many readers the most interesting parts of this book will be the accounts of the habits of the types discussed.

It is unfortunate that this book did not appear a few years ago when so many military personnel were going to Pacific areas. However, those who have spent time in the Pacific will find this book particularly interesting.—*D. J. Borror.*

Reptiles of the Pacific World, by Arthur Loveridge. The Macmillan Company, New York, 1945. xii+259 pp. $3.00.